The Response of Juvenile Coho and Chinook Salmon Stocks to Salmon Spawner Abundance: Marine Nutrients as Drivers of Productivity

By

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Abstract

Resource subsidies from spawning Pacific salmon (*Oncorhynchus* spp.) in the form of marine-derived nutrients (MDN) benefit juvenile salmonids while they rear in fresh water, but it remains unclear if the abundance of spawners in a watershed affects the productivity of salmon stocks that rear in those riverine systems. This dissertation aimed to provide a better understanding of these dynamics by evaluating whether the response of juvenile salmon to MDN is sufficient to enhance overall stock productivity. In Chapter 1, I examined correlative relationships in the abundance of Pink (*O. gorbuscha*) and Coho (*O. kisutch*) salmon and simulated spawner-recruit dynamics to determine if those correlations were produced by a Coho Salmon response to marine subsidies from Pink Salmon, a shared response to marine conditions, and/or autocorrelations in the returns of both species. Results demonstrated that observed correlative patterns most closely resembled simulated freshwater effects, providing evidence that marine subsidies from Pink Salmon influence Coho Salmon productivity. In Chapter 2, I examined the relationship between spawner abundance and MDN assimilation by juvenile Coho and Chinook (*O. tshawytscha*) salmon in the Unalakleet River watershed. Stable isotope analysis demonstrated that after salmon spawned, MDN assimilation by juvenile salmon in the fall was a function of adult Pink and Chinook salmon spawner abundance, regardless of the habitat occupied by rearing juveniles. However, by the following summer, high retention of MDN in complex habitat masked seasonality of MDN assimilation in sloughs and river sections with abundant lentic-lotic exchanges. As such, MDN assimilation in the summer (prior to arrival of spawners) bore only a faint relationship to spawner abundance and distribution from the previous year. In chapter 3 I examined the relationship between MDN assimilation (Chapter 2) and juvenile salmon growth, size, body condition, and abundance. Prior to salmon spawning, residual MDN from past years offered little advantage to juvenile salmon. However, after the arrival of spawning salmon, MDN enhanced juvenile salmon size, growth, and condition in fall and winter. The collective results from this dissertation thus provides compelling evidence that MDN from spawning Pink Salmon may enhance the productivity of Coho and Chinook salmon. Management

agencies should explore modified spawner-recruit models that incorporate MDN relationships to determine if they more accurately describe population dynamics. Where they do, such models may be used to forecast salmon returns and possibly adjust escapement goals (the number of spawners desired on the spawing grounds) to improve maximum-sustained yields (MSY).

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INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) accumulate over 99% of their adult mass while growing at sea and return massive amounts of marine carbon, nitrogen, and other nutrients (marine-derived nutrients; MDN) when returning to spawn and die in fresh water. Marine subsidies from spawning salmon are assimilated into freshwater and terrestrial food webs and can have large effects on multiple trophic levels. For example, MDN from carcasses and fish excretion can stimulate stream biofilms and increase microbial productivity (Bilby et al. 1996; Wipfli et al. 1998; Gende et al. 2002; Mitchell and Lamberti 2005). Riparian vegetation, soil, and insect communities become enriched in MDN (Ben-David and Schell 1998; Reimchen et al. 2002; Hocking and Reimchen 2009), and terrestrial scavengers, including birds, bears, and wolves feed on salmon and disperse nutrients in the riparian zone (Hilderbrand et al. 1999; Adams et al. 2010). Within aquatic food webs, freshwater consumers, including juvenile salmon and other fishes, benefit from MDN through a variety of trophic pathways.

Pulsed marine subsidies are incorporated into juvenile salmon diets through both direct and indirect routes and can increase the quantity and quality of juvenile salmon diets by providing large, energy rich diet items. Juvenile salmon feed directly on eggs and carcasses during the spawning season (Bilby et al. 1998; Pearsons and Fritts 1999; Armstrong et al. 2010) and on fry and smolt in the spring (Parker 1971; Hargreaves and LeBrasseur 1985; Ruggerone and Rogers 1992; Denton et al. 2009). Indirectly, nitrogen and phosphorous from decaying carcasses are incorporated into aquatic and riparian food webs, thus increasing primary production and bolstering invertebrate communities (Wipfli et al. 1999, 2003; Chaloner et al. 2004; Hicks et al. 2005; Lang et al. 2006). Moreover, invertebrates colonize and feed on salmon carcasses thus increasing the size and abundance of potential food items such as midge larvae (family Chironomidae; Chaloner et al. 2004; Hicks et al. 2005), caddisflies (order Trichoptera; Winder et al. 2005; Hicks et al. 2005), stoneflies (order Plecoptera; Ellis 1970; Wipfli et al. 1998), and blowflies (family Calliphoridae; Armstrong et al. 2010).

Access to marine subsidies has been shown to increase growth rates and improve overall condition in individual juvenile salmon in localized settings. Studies throughout the Pacific Northwest and Alaska have highlighted the benefit of densely spawning species such as Pink (*O. gorbuscha*), Chum (*O. keta*), and Sockeye (*O. nerka*) salmon to other salmonid species that rear in freshwater (Bilby et al. 2003; Wipfli et al. 2010; Rinella et al. 2012). Juvenile Coho Salmon exhibited increased growth (Wipfli et al. 2003; 2010) and lipid content (Heintz et al. 2004, 2010) in response to Pink Salmon carcasses, and Coho Salmon and Dolly Varden (*Salvelinus malma*) also demonstrated elevated growth rates and energy content with increasing salmon spawning density in Southcentral Alaska streams (Rinella et al. 2012). Sockeye Salmon in southwest Alaska have been shown to benefit stream dwelling salmonids, including Coho Salmon, Dolly Varden, and Rainbow Trout (*O. mykiss*), by increasing ration size, body condition, and growth (Scheuerell et al. 2007; Denton et al. 2009; Armstrong et al. 2010).

Factors that substantially affect juvenile salmon growth, size, lipid reserves, and overall body condition have the potential to ultimately affect overall stock productivity by increasing survival of juveniles while in fresh water. Productivity of salmon stocks is frequently described as recruitment to the spawning adult life stage, relative to the number of spawners in the parent generation. Recruitment, in turn, is largely determined by both the abundance and survival of juveniles (Quinn 2005). Higher freshwater survival rates ultimately increase smolt abundance and consequently have strong potential to influence productivity (Ebersole et al. 2006). Indeed, Coho Salmon productivity in particular is thought to be limited mainly by the quality and quantity of freshwater resources (Bradford et al. 1997; 2000). Survival of juvenile salmon in fresh water is partially a product of body size and condition as larger fish with greater lipid reserves demonstrate higher survival rates during periods of food shortages, and in particular during over-wintering periods (Quinn and Peterson 1996; Zabel and Achord 2004; Brakensiak and Hankin 2007; Pess et al. 2011). Fish size also provides competitive advantages as larger fish are less prone to predation (Sogard 1997), less likely to suffer from disturbances such as flooding (Pearsons et al. 1992; Bell et al. 2001; Pess et al. 2011), and are more competitive in defending preferred feeding stations

(Ejike and Schreck 1980; Reinhardt 1999; Nielsen 1992; Rosenfeld and Hatfield 2006). In addition to affecting freshwater survival rates, factors that affect smolt size may further influence marine survival rates given that size-selective mortality can be particularly strong during the early marine portion of the life cycle (Holtby et al. 1990; Beamish et al. 2004; Duffy and Beauchamp 2011). Furthermore, juvenile salmon survival is related to lipid stores (often approximated by condition indices) (Biro et al. 2004; Rinchard et al. 2007) that allow animals to store temporarily abundant resources from pulsed subsidies, including MDN from spawning salmon, for later use when food is scarce (Heintz et al. 2010). Frequently, over-winter survival rates are directly related to lipid reserves which may impact overall productivity (Cunjak 1996; Cunjak et al. 1998; Post and Parkinson 2001; Biro et al. 2004; Finstad et al. 2004; Rinchard et al. 2007).

While the effects of MDN on juvenile fish growth and size has been well documented, linking MDN levels to broader productivity of salmon populations has proven difficult (Uchiyama et al. 2008; Maxwell et al. 2006; Adkison 2010; Schindler et al. 2005). Given how MDN has been shown to improve juvenile salmon growth and condition, it is reasonable to hypothesize that these effects ultimately influence stock productivity. Much of the population-scale research to date has occurred on lake rearing Sockeye Salmon with sometimes inconclusive results (Schindler et al. 2005; Uchiyama et al. 2008; Adkison 2010). Population studies on stream rearing salmonids, such as Coho and Chinook (*O. tshawytscha*) salmon, have been more limited but have nevertheless supported the notion that MDN effects have population level consequences. With respect to the freshwater phase of their life cycle, the abundance of juvenile Coho Salmon was positively related to adult Pink Salmon abundance in British Columbia streams (Nelson and Reynolds 2014) while Coho Salmon smolt abundance in Washington state rivers was correlated with Pink Salmon escapements in the year prior to smolting (Zimmerman 2011). In terms of adult populations, Pink Salmon escapements during Coho Salmon freshwater residency were a better predictor of Coho Salmon recruitment than was Coho Salmon spawner abundance in a small (25 km^2) watershed in Southeast Alaska (Shaul et al. 2014). Similarly, in the Skagit River, Washington state, Coho

Salmon productivity was correlated with Pink Salmon spawning biomass in the year Coho Salmon reared in freshwater (Michael 1995). While these studies match expectations, the MDN dynamics within these systems were not investigated.

The limited research scaling up MDN effects to population and watershed levels has left a gap in our understanding of the response of juvenile salmon stocks to the abundance of spawning adult salmon within a watershed (Piccolo et al. 2009; Bernard and Clark 2009). Much of the research to date has been limited in duration and has not focused on identifying quantitative relationships between spawner abundance and the response of juvenile salmon populations (Piccolo et al. 2009). Indeed, despite the pulsed timing of spawning, MDN assimilation in some fish populations lacks a seasonal pattern (Rinella et al. 2013) making it unclear if or how juvenile salmon MDN assimilation relates to annual estimates of spawner abundance. Given that an environmental variable must have a large influence on recruitment to influence stock level productivity (Adkison 2009), one would expect to observe relationships between metrics of spawner biomass and factors affecting salmon productivity if MDN processes were enhancing stock productivity.

Salmon escapements, or the number of adult salmon surviving to spawn, are monitored along the Pacific coast via counting towers, weirs, sonars, and aerial and foot surveys. In addition to providing data to model harvestable surplus and set sustainable escapement goals (Munro and Volk 2015), they also provide a metric of MDN imported to freshwater systems. For MDN processes to be considered in salmon management plans, MDN assimilation in juvenile salmon should be predictably related to escapement estimates and result in enhanced size, body condition, survival, and abundance. Ultimately relating this cascade of relationships to escapement estimates in a manner that may be useful to fisheries managers will require developing quantitative predictions and further case-specific studies of how juvenile salmon respond to spawner abundance at the population level.

To better understand how juvenile salmon populations respond to the abundance of spawning salmon via MDN processes will require addressing several gaps in our knowledge. Initially, we must understand

how MDN assimilation by rearing juveniles relates to the biological characteristics of escapements, including species composition and abundance of spawners, timing of spawning events, and location and habitat of both spawners and rearing juveniles (Piccolo et al. 2009). Following this, we need to understand how MDN assimilation by juvenile salmon populations results in nutritional benefits that can affect survival rates, including increased growth, size, and body condition. Finally, we need to understand if and how those nutritional benefits affect the abundance of rearing juveniles and outmigrating smolts, and subsequent recruitment to the adult life stage.

This dissertation sought to address these knowledge gaps by focusing on a region in western Alaska where ongoing salmon monitoring projects and a relatively small watershed provided an opportunity to examine Coho and Chinook salmon responses to escapement estimates of all salmon migrating into the watershed. In this dissertation I; 1) determined if relationships between Coho and Pink salmon abundance in Norton Sound were best explained by an MDN benefit of Pink Salmon to Coho Salmon; 2) examined how MDN assimilation in juvenile salmon related to the biological characteristics of the Unalakleet River escapements (species composition and abundance of spawners, timing of spawning events, and location and habitat of spawners); and 3) determined how MDN assimilation by juvenile Coho and Chinook salmon affected growth, body condition, and the abundance of juvenile salmon emigrating from the watershed. In Chapter 1 I examined correlations in the abundance of adult Coho and Pink salmon in escapement and harvest data of the two species to determine if Coho Salmon productivity was enhanced by Pink Salmon escapements or if alternate hypotheses provided the best explanation. I examined escapement and harvest data from several rivers in the Norton Sound region of western Alaska as well as from a system in Southeast Alaska where independent studies have documented MDN relationships between Coho and Pink salmon. In Chapters 2 and 3 I present a case study of one of the Norton Sound systems, the Unalakleet River, to examine how escapements of Pink, Chum, Chinook, and Coho salmon related to MDN assimilation and subsequent benefits in rearing Coho and Chinook salmon. Specifically in Chapter 2 I examined how MDN assimilation by rearing juvenile Coho and Chinook salmon related to

the biological characteristics of the escapement (including salmon species, abundance, and distribution) and macro-habitat features of the watershed. In Chapter 3 I examined how MDN assimilation by juvenile salmon enhanced their growth, size, and condition throughout the watershed and examined the abundance and age structure of Coho Salmon smolts emigrating from two sub-drainages of the Unalakleet River watershed. This dissertation was intended to evaluate whether escapements provide a useful metric of watershed-scale MDN that substantially and predictably enhances productivity of salmon stocks. It is my intention that this work will provide a foundation for developing revised management plans that incorporate MDN relationships into improved multi-species spawner-recruit models.

Literature Cited:

Adams, L. G., S. D. Farley, C. A. Stricker, D. J. Demma, G. H. Roffler, D. C. Miller and R. O. Rye. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? Ecological Applications 20: 251-262.

Adkison, M. A. 2010. Models of the effects of marine-derived nutrients on salmon (*Onchorhynchus* spp.) population dynamics. Canadian Journal of Fisheries and Aquatic Science 67: 5-15.

Adkison, M. A. 2009. Drawbacks of complex models in frequentist and Bayesian approaches to natural-resource management. Ecological Applications, 19: 198-205.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91: 1445-1454.

Beamish, R. J., C. Mahnken and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. Transactions of the American Fisheries Science 133: 26-33.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bell, E., W. G. Duffy and T. D. Roelofs. 2001. Fidelity and survival of juvenile Coho Salmon in response to a flood. Transactions of the American Fisheries Science 130: 450-458.

Bernard, D. R., and R. A. Clark. 2009. Importance of marine-derived nutrients in establishing escapement goals for Pacific salmon. American Fisheries Society Symposium 71: 147-164.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Science 53: 164-173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Science 55:1909-1918.

Bilby, R. E., E. W. Beach, B. R. Fransen, J. K. Walter, and P. A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of the American Fisheries Society 132: 733-745.

Biro, P. A., A. E. Morton, J. R. Post and E. A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Science 61: 1513-1519.

Bradford, M. J., R. A. Myers, and J. R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production Canadian Journal of Fisheries and Aquatic Science 57: 677-686.

Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society 126: 49-64.

Brakensiak, K. E., and D. G. Hankin. 2007. Estimating overwinter survival of juvenile Coho Salmon ina northern California stream: accounting for effects of passive interated transponder tagging mortality and size-dependent survival. Transactions of the American Fisheries Society 136: 1423-1437.

Chaloner, D. T., G. A. Lamberti, R. W. Merritt, N. L. Mitchell, P. H. Ostrom and M. S. Wipfli. 2004 Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshwater Biology 49: 587-599.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Science 53(Suppl. 1): 267-282

Cunjak., R. A., T. D. Prowse and D. L. Parrish. 1998. Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent"? Canadian Journal of Fisheries and Aquatic Science 55(Suppl. 1): 161-180.

Denton, K. P., H. B. Rich Jr., and T. P. Quinn. 2009. Diet, movement, and growth of Dolly Varden in response to Sockeye Salmon subsidies. Transactions of the American Fisheries Society 138: 1207-1219.

Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Science 68: 232-240.

Ebersole, J. L., P. J. Wigington Jr., J. P. Baker, M. A. Cairns, M. R. Robbins Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton and S. G. Leibowitz. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. Transactions of the American Fisheries Society 135: 1681-1697.

Ejike, C. and C. B. Schreck. 1980. Stress and Social Hierarchy Rank in Coho Salmon. Transactions of the American Fisheries Society 109: 423-426.

Ellis, R. J. 1970. Alloperla stonefly nymphs: predators or scavengers on salmon eggs and alevins? Transactions of the American Fisheries Society 99: 677-683.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. Bioscience 52: 917-928.

Hargreaves, N. B. and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Canadian Journal of Fisheries and Aquatic Science 42: 659-668.

Heintz, R. A., B. D. Nelson, J. Hudson, M. Larson, and L. Holland. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Transactions of the American Fisheries Society 133: 559-567.

Heintz, R. A., M. S. Wipfli, and J. P. Hudson. 2010. Identification of marine-derived lipids in juvenile coho salmon and aquatic insects through fatty acid analysis. Transactions of the American Fisheries Society 139: 840-854.

Hicks, B. J., M. S. Wipfli, D. W. Lang and M. E. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144: 558-569.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins and C. C. Schwartz. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121: 546-550.

Hocking, M. D., and T. E. Reimchen. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. Oikos 118: 1307-1318.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 47: 2181-2194.

Lang, D. W., G. H. Reeves, J. D. Hall, and M. S. Wipfli. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. Canadian Journal of Fisheries and Aquatic Science 63: 917-930.

Maxwell, M. R., R. M. Peterman, M. J. Bradford and E. A. MacIsaac. 2006. A Bayesian analysis of biological uncertainty for a whole-lake fertilization experiment for sockeye salmon in Chilko Lake, British Columbia, and implications for the benefit-cost ratio. N. Am. J. Fish. Man. 26:418-430.

Michael Jr., J. H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Science, 69: 228-233.

Mitchell, N. L. and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. Limnology and Oceanography 50: 217-227.

Munro, A. R. and E. C. Volk. 2015. Summary of Pacific salmon escapement goals in Alaska with a review of escapements from 2006 to 2014. Alaska Department of Fish and Game, Fishery Manuscript Series No. 15-34, Anchorage.

Nelson, M. C. and J. D. Reynolds. 2014. Time-delayed subsidies: interspecies population effects in salmon. PLoS ONE 9(6): e98951.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121: 617-634.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28: 1503-1510.

Pearsons, T. N. and A. L. Fritts. 1999. Maximum size of chinook salmon consumed by juvenile coho salmon. North American Journal of Fisheries Management 19: 165-170.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemlages. Transaction of the American Fisheries Society 121: 427-436.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson and T. P. Quinn. 2011. The influence of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. Transaction of the American Fisheries Society 140: 883-897.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Linking Alaskan salmon fisheries management with ecosystem-based escapement goals: a review and prospectus. Fisheries 34: 124-134.

Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. American Fisheries Society in association with University of Washington Press. Seattle, WA.

Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Science 53: 1555-1564.

Reimchen, T. E., D. Mathewson, M. D. Hocking, J. Moran, and D. Harris. 2002. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in riparian zones in coastal British Columbia. American Fisheries Society Symposium XX: 1-12.

Reinhardt., U. G. 1999. Predation risk breaks size-dependent dominance in juvenile coho salmon (*Oncorhynchus kisutch*) and provides growth opportunities for risk-prone individuals. Canadian Journal of Fisheries and Aquatic Society 56: 1206-1212.

Rinchard, J. S. Czesny and K. Dabrowski. 2007. Influence of lipid class and fatty acid deficiency on survival, growth, and fatty acid composition in rainbow trout juveniles. Aquaculture 264: 363-371.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Science 69: 73-84.

Rinella, D. J., M. S. Wipfli, C. M. Walker, C. A. Stricker and R. A. Heintz. 2013. Seasonal persistence of marine-derived nutrients in south-central Alaskan salmon streams. Ecosphere 4: 1-18.

Rosenfeld, J. S and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Society 63: 683-698.

Ruggerone, G. T. and D. E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: implications for salmon management. North American Journal of Fisheries Management 12: 87-102.

Scheuerell, M. D., J. W. Moore, D. E. Schindler and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52: 1944-1956.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology, 86 (12), 3225-3231.

Shaul, L. D., K. F. Crabtree, K. C. Koolmo, K. M. Koolmo, J. V. Nichols, and H. J. Geiger. 2014. Studies of coho salmon and other *Oncorhynchus* species at Ford Arm Creek, 1982 – 2009. Alaska Department of Fish and Game, Fishery Manuscript Series No. 14-02, Anchorage.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.

Uchiyama, T., B. P. Finney, and M. D. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Onchorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Science 65: 1635-1648.

Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Canadian Journal of Fisheries and Aquatic Science 62:2285-2293.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Science 55: 1503-1511.

Wipfli, M. S., J. Hudson, D. T. Chaloner and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Science 56: 1600-1611.

Wipfli, M. S., J. P. Hudson, J. P. Caouette and N. L. Mitchell. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic lveles in streamside experimental channels. Transactions of the American Fisheries Society 139: 824-839.

Zabel, R. W. and S. Achord. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. Ecology, 85; 795-806.

Zimmerman, M. 2011. 2011 wild coho forecasts for Puget Sound, Washington Coast, and Lower Columbia. Washington Department of Fish and Wildlife, Olympia, Washington.

Chapter 1: Disentangling autocorrelation from marine-subsidy and ocean effects: do Pink Salmon escapements affect Coho Salmon productivity?

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Abstract

Covarying population dynamics of Pink (*Oncorhynchus gorbuscha*) and Coho (*O. kisutch*) salmon have been interpreted as a Coho Salmon response to marine subsidies from Pink Salmon (freshwater effects), a shared response to marine conditions (ocean effects), or arising from autocorrelation. To examine how different effects give rise to different correlative patterns we simulated Pink and Coho salmon population dynamics in a spawner-recruit model that included ocean and freshwater effects and various levels of autocorrelation, measured five different Coho-Pink salmon correlations in each simulation, and compared simulated R^2_{Adj} values to those present in real-world brood tables. Autocorrelations in combination (either at multiple lags or in the two species) produced correlations between the two species even in the absence of biological interactions. However, freshwater effects produced stronger correlations between Coho Salmon returns and Pink Salmon escapements, while ocean effects produced strong correlations between escapements of the two species. Correlative patterns observed in western Alaskan stocks most closely resembled simulated freshwater effects, providing evidence that marine subsidies from Pink Salmon influence Coho Salmon productivity in this region.

Introduction

North America's Pacific salmon (*Oncorhynchus* spp.) fisheries are currently managed by monitoring the number of adult spawners (escapement) and modeling the relationship between escapements and subsequent returns (recruitment, or the number of adults returning to spawn, including those intercepted by fisheries) in a density-dependent framework (Beverton and Holt 1957; Ricker 1975, Haught et al. 2017). Modeling salmon recruitment is often constrained by the amount and quality of data, and even the best data show high variability in recruitment rates attributable to both freshwater and marine conditions (Peterman et al. 1998; Needle 2002). Identifying factors that significantly improve the fit of these models and discriminating between freshwater and ocean effects on returns may allow managers to better manage and forecast salmon runs.

Marine derived nutrients (MDN) imported to freshwater systems by migrating adult salmon can affect growth and survival of juvenile salmon rearing in fresh water (Bilby et al. 1996, 1998; Wipfli et al. 1999, 2003) and correlations between Coho Salmon (*O. kisutch*) returns or returns/spawner and Pink Salmon (*O. gorbuscha*) escapements in the years when Coho Salmon were rearing in fresh water suggest a benefit of MDN from spawning Pink Salmon to Coho Salmon. Given the life cycle of Coho Salmon, MDN benefits may be pronounced because Coho Salmon spend a large portion (50–75%) of their life cycle in fresh water, and overall productivity is thought to be limited by freshwater conditions (Bradford et al. 1997, 2000). One such relationship was documented in Ford Arm Creek, Southeast Alaska, where Pink Salmon abundance during Coho Salmon freshwater residency was a better predictor of Coho Salmon returns than were Coho Salmon escapements (Shaul et al. 2014). Similarly, Coho Salmon returns-per-spawner in the Skagit River, Washington State, were correlated with Pink Salmon spawning biomass in the year Coho Salmon reared in fresh water (Michael 1995). Direct measurements of smolt abundance (the number of juvenile salmon emigrating to the ocean) in the Skagit and other Washington state rivers has shown Coho Salmon smolt production to be strongly correlated with Pink Salmon escapements (Zimmerman 2011), lending further credence to MDN-based explanations.

In contrast, a relationship between adult returns of the two species has been interpreted as a similar response to ocean conditions. In this relationship, commercial harvests of the two species were strongly correlated between 1955 and 2005 (Shaul et al. 2007). Coho Salmon in Southeast Alaska have considerable overlap with Pink Salmon in marine waters during their first summer at sea (Weitkamp et al. 2011) and the abundance of Pacific salmon species demonstrated similar trends at the scale of ocean basins (Stachura et al. 2014). Furthermore, Pink Salmon smolt may function as a predator buffer for Coho Salmon smolt during early marine residency (LaCroix et al. 2009), although more recent evidence has cast doubt on this effect (Shaul and Geiger 2016).

In addition to possible biological causes for observed trends, autocorrelation alone could produce these patterns. Autocorrelation in salmon time-series data occurs when environmental effects on spawner-recruit relationships that span multiple years produces successive years of poor or good productivity (Quinn and Deriso 1999). If two populations were to trend in the same direction over a period of time, independently of biological mechanisms linking the two species, the observed correlations could arise by chance. Autocorrelation is typically addressed by adjusting degrees of freedom or by statistically removing it before analysis (Pyper and Peterman 1998). However, autocorrelation reflects low-frequency processes that are important sources of covariation in fish recruitment and even if biological mechanisms are present, they co-exist with autocorrelative processes, making interpretation of observed patterns problematic (Pyper and Peterman 1998).

Understanding the causal nature of Coho-Pink salmon relationships would be valuable to the management of both species but when only adult data are available (Michael 1995, Shaul 2007), it is unclear which hypothesis (MDN, ocean conditions, or autocorrelation), if any, is most supported. Different correlative patterns might result from altogether dissimilar biological processes and occur independently of each other. Conversely, a single biological process might produce multiple correlations and the various patterns are simply different manifestations of the same phenomenon. Given the life history of Pink Salmon (zero years in fresh water and one at sea) and Coho Salmon (one to three years in fresh water

followed by one year at sea), and the presence of even-year dominance in many Pink Salmon populations (even and odd year Pink Salmon are distinct populations with even year runs in western Alaska often many times larger than odd year runs) (Menard et al. 2013), it is unclear how these effects would manifest in correlations between adults of the two species. Indeed, discriminating between these hypotheses may not be possible without long term smolt data in conjunction with adult return data. Misinterpreting these relationships could result in misdirected research and faulty management decisions, while ignoring meaningful patterns would represent a missed opportunity for improved salmon forecasting and management.

To investigate the cause of correlations evident in Pink and Coho salmon time series, we simulated population dynamics under multiple competing hypotheses to determine the most likely explanation for observed patterns. The objective of this study was to determine whether similar trends in adult Coho and Pink salmon return and escapement data are best explained by: (1) a marine-subsidy effect of Pink Salmon on Coho Salmon (freshwater effects), (2) a correlated response by the two species to the marine environment (ocean effects), (3) autocorrelation in one or both species, or (4) some combination of these effects. To explore our hypotheses, we measured five correlations relating Pink and Coho salmon brood tables from Ford Arm Creek in Southeast Alaska and four rivers (North, Kwiniuk, Niukluk, and Nome Rivers) in Norton Sound, western Alaska. Based on two paired populations of Coho and Pink salmon, from Ford Arm Creek in SE Alaska (Shaul et al. 2014) and the North River in Norton Sound (Menard et al. 2013), spawner-recruit models were used to simulate these hypotheses and determine which effects produced correlations between adult Coho and Pink salmon (Shaul et al. 2007, Michael 1995). Simulation results were examined for correlations between Pink and Coho salmon similar to those present in the Norton Sound rivers and Ford Arm Creek to determine the most likely explanation for these observed relationships.

Materials and Methods

Study areas: Ford Arm Creek (55.600^0 N, 135.883^0 W) lies 72 km north of Sitka, Alaska and connects Ford Arm Lake to the Gulf of Alaska (Figure 1.1). Ford Arm is located on the outer coast of Chichagof Island in Southeast Alaska and the lake and creek drain approximately 25 km^2 of mountainous, temperate rainforest. The watershed is populated by Pink, Coho, Chum (*O. keta*), and Sockeye (*O. nerka*) salmon (Shaul et al. 2014). Pink Salmon are the most dominant by biomass followed by Chum Salmon. Coho and Sockeye salmon are the least dominant and occur in similar numbers (Shaul et al. 2014).

The North River is the largest tributary of the Unalakleet River, which drains into the eastern end of Norton Sound in western Alaska (63.878°N, 160.605°W) (Figure 1.1). The North River drains approximately 1,280 km^2 of the Nulato Hills, is characterized by a subarctic climate and hilly to mountainous terrain with alpine tundra in the highlands and high brush in the lowlands. The river supports populations of Chinook (*O. tshawytscha*), Coho, Chum, Pink, and Sockeye salmon. In terms of biomass, Pink Salmon are the most dominant species in the system, followed by Coho and Chum salmon in similar abundance. Chinook Salmon constitute less than 2% of the annual anadromous biomass while the Sockeye Salmon stock is trivial (Menard et al. 2013).

The Kwiniuk, Niukluk, and Nome rivers are located on the Seward Peninsula in western Alaska and drain into the northern edge of Norton Sound (Figure 1.1). The Kwiniuk River watershed encompasses approximately 570 km^2, the Niukluk River watershed approximately 4,980 km^2 and the Nome River approximately 420 km^2. These rivers are similar to the North and Unalakleet rivers in climate, topography, and relative abundance of Pacific salmon (Menard et al. 2013).

North River run reconstructions: To model and simulate spawner-recruit relationships between Coho and Pink salmon, we reconstructed the historical brood year returns for the two species using escapement (adult spawners), harvest and, where available, age class data. North River Coho and Pink salmon runs were reconstructed using escapement data from a counting tower on the North River and harvest data from the Alaska Department of Fish and Game (ADF&G) (Menard et al. 2013). Harvest of Pink Salmon

in the North and Unalakleet rivers is negligible in relation to escapement, so total Pink Salmon returns were considered equal to escapements (Menard et al. 2013). Pink Salmon have a two-year life cycle, so returns for a brood year were simply calculated as the number of adults returning two years after the brood year (Table 1.A.1).

Coho Salmon runs were reconstructed using the North River tower counts and sport, commercial, and subsistence fisheries harvests from the Unalakleet River and Unalakleet commercial fishing subdistrict (Figure 1.1) (Menard et al. 2013). Because the North River tower sometimes failed to count through the entire Coho Salmon spawning migration, tower counts were inflated proportional to the amount of the run counted as determined by historical run timing past the counting tower through September 15th (Table 1.A.2; maximum expansion was 1.52 in two years and 1.16 or less otherwise). The North River is a tributary of the Unalakleet River, and the bulk of the Coho Salmon harvest in marine and subsistence fisheries has occurred in marine waters near the mouth of the river (Figure 1.1). These fisheries are assumed to intercept other stocks (in particular, Yukon River stocks that migrate through Norton Sound), and for purposes of this run reconstruction, 75% of the harvest was assumed to be Unalakleet River stocks (an approximation based on conversations with local fishermen). Given that exploitation (the proportion of returning adults harvested in fisheries) in the region is generally around 30% (Menard et al. 2013), our analysis was driven primarily by escapement estimates (analyses indicated that changing harvest proportions did not affect results; data not shown). Of the harvest, 12.6% was deemed to be bound for the North River based on ADF&G telemetry studies of migrating Coho Salmon (Joy and Reed 2007). Thus, North River harvests were calculated as 0.75*0.126*Coho Salmon harvest (Appendix A11 of Menard et al. 2013; Table 1.A.2). Total returns for each year were calculated as the sum of the North River tower counts plus the North River harvest. Returns were ascribed to brood year based on the age structure of Coho Salmon harvested in the commercial fishery (Soong et al. 2008) or, if actual age estimates were not available, by the average age structure from the last three years that age estimates were available (Table 1.A.2).

Ford Arm Creek run reconstruction: Ford Arm Creek run reconstructions were derived using data reported by Shaul et al. (2014). Pink Salmon escapement data consisted of peak aerial escapement counts in Ford Arm Creek multiplied by an expansion factor of 2.5 to estimate total escapement (Shaul et al. 2014). Although peak aerial escapement counts have flaws (Jones et al. 1998), Ford Arm Creek is relatively small and Shaul et al. (2014) expressed confidence in their expansion factor based on published (Jones et al. 1998) and unpublished calibrations, as well as over two decades worth of observations (Shaul et al. 2014). The Ford Arm Pink Salmon index comprised 30% of the Slocum Arm Pink Salmon index (Shaul et al. 2014), and thus annual harvests were modeled as 30% of the Khaz Bay purse seine fishery harvest, which comprises the bulk of the Slocum Arm harvest. Total Pink Salmon returns for a given brood year were calculated by adding the escapement and estimated harvest two years later (Table 1.A.3). Ford Arm Creek Coho Salmon escapements were estimated from a mark-recapture estimate of the number of adults that passed a weir. Run reconstructions and brood tables for Ford Arm Coho Salmon, including smolt production and survival data, were taken directly from Shaul et al. (2014).

Norton Sound run reconstructions: Coho and Pink salmon runs for the Kwiniuk, Niukluk, and Nome rivers (Figure 1.1) were reconstructed with data from ADF&G Fisheries Management Reports (Menard et al. 2013). Additionally, the Norton Sound region as a whole was examined using composite escapements and harvests (Appendix A19 and A20 in Menard et al. 2013). Salmon escapements were estimated from counting tower data. Pink Salmon tower counts were considered complete, but Coho Salmon counts often failed to count the entire Coho Salmon run during some years due to high water common in the fall. Most (> 90%) of the Coho Salmon spawning migration has entered the rivers by September 1st, and where tower counts ended before September 1st, escapement estimates were revised upwards relative to the proportion of the run counted. Of the three systems examined, 22% of the counts ended before September 1st and 12% ended before August 25 (Menard et al. 2013).

Salmon harvest data were derived from harvests reported by fishing districts in Norton Sound (Figure 1.1). Commercial and subsistence harvests on the Seward Peninsula typically occur in marine waters and

are recorded for the fishing district as a whole. As such, it is unknown what portion of subdistrict harvests were bound for a particular drainage. To reconstruct salmon runs in these three rivers, the proportion of the subdistrict harvest ascribed to the drainage of interest was based on the number of spawning drainages located in the subdistrict. Thus, the Nome River proportion of the Nome subdistrict harvest was assumed to be 0.25 based on four other spawning drainages in the subdistrict and the Niukluk River harvest proportion was assumed to be 0.5 based on two spawning drainages in the Golovin subdistrict (Figure 1.1). The Kwiniuk River harvest proportion was assumed to be 0.6 based on two other spawning drainages in the Elim subdistrict and recognizing that the Kwiniuk River is the closest drainage to Elim, the community where the bulk of the fishermen reside (Figure 1.1). The same range of values was used for both Pink and Coho salmon run reconstructions. Although these harvest proportions are highly uncertain, changing the assumed proportions resulted in abundance estimates that produced cross-species correlations very similar to those seen here (not shown). For each scenario, total returns were calculated by adding escapement and estimated harvest.

Harvest of Pink Salmon in Norton Sound are negligible in relation to escapements, so total Pink Salmon returns were considered equal to escapements, and returns for a brood year were calculated as the returns occurring two years after the brood year (Menard et al. 2013). Coho Salmon returns from a given brood year were calculated by assigning annual returns (escapements plus harvest) to the appropriate brood year based on a fixed age structure calculated from the average age structure in the North River and typical of the Norton Sound region (Soong et al. 2008), as empirical age data were not available for these rivers. Thus 11% of annual returns were assigned as 3-year-olds, 81% assigned as 4-year-olds and 8% assigned as 5-year-olds. Although this ignored variability in yearly age structure, it maintained the relative importance of age-2.1 fish to determining brood year returns. Using fixed-age models for salmon run reconstructions causes returns from large and small escapements to be over- and underestimated, respectively, thus reducing contrast in the data set (Zabel and Levin 2002). This would lead to a more conservative analysis because the probability of detecting the various correlations would be reduced as

extreme values are dampened. Run reconstructions were performed for the Norton Sound composite data and for each of the three rivers for each of the three harvest scenarios described above.

Correlations between Pink and Coho salmon: To investigate how correlations between Pink and Coho salmon populations would be produced by freshwater effects, ocean effects, and autocorrelation we measured several previously described correlations between Pink and Coho salmon (Michael 1995; Shaul et al. 2007, 2014) along with new correlations proposed here (Table 1.1). Correlations between Coho Salmon returns and Pink Salmon escapements during the years that Coho Salmon reared in freshwater (the years following spawning by the parent generation) were expected to arise if Pink Salmon benefitted Coho Salmon production via marine nutrients. We also examined a correlation in the adult abundance of both species that was expected to arise from ocean conditions given that both species spend one year in the ocean prior to spawning. Autocorrelation was expected to produce some of these correlations by chance and it was unclear if ocean and freshwater effects could give rise to unexpected correlations. The correlations we propose were the $Return_1$ correlation, which described Coho Salmon returns from brood year t (the year the parent generation spawned) as a function of Pink Salmon escapements in year $t+1$, and the $Return_{12}$ correlation, which described Coho Salmon returns from brood year t as a function of Pink Salmon escapements in year $t+1$ and $t+2$. The *Prod* correlations ($Prod_1$ and $Prod_{12}$), based on Michael (1995), were similar to the *Return* correlations, but with returns-per-spawner (R_t/S_t) replacing returns (R_t) as the dependent variable. Following Shaul et al. (2007), the *Marine* correlation described the relationship between Coho and Pink salmon escapements in the same year. Although Shaul et al. (2007) originally examined harvests, Pink Salmon harvests in Norton Sound are negligible and thus we chose to examine escapements. Examining total returns was another option, but would not change our results and conclusions as Pink Salmon harvests were a random variable in our simulations. Consequently, examining total returns would add more variation to Ford Arm simulation results without changing the actual effects (freshwater, ocean or autocorrelative) that would cause correlations between either annual returns or escapements of the two species.

For each data series these five correlations were calculated in addition to autocorrelations in the Coho and Pink salmon return data. For each of the five correlations (Table 1.1), the adjusted R^2 value (R^2_{Adj})was calculated using standard linear models (Neter et al. 1996) with Pink Salmon as the independent variables and Coho Salmon as the dependent variables. First and second lag autocorrelations were estimated for annual Coho and Pink salmon returns using standard statistical procedures (Venables and Ripley 2002). For the purposes of measuring correlations (Table 1.1) an anomalous year in the Ford Arm Pink Salmon escapement data was omitted as it represented a very high Pink Salmon escapement (twice that of the next highest escapement). During that year, surveys showed huge numbers of Pink Salmon at the mouth but far fewer than would normally be expected in the stream proper, suggesting that escapement estimates that year did not accurately reflect the biomass of MDN imported to the system (Leon Shaul, *pers. comm.*).

Simulation Model: We used a Ricker spawner-recruit model (Ricker 1975) to describe Pink Salmon population dynamics, where the number of adults returning to spawn (returns, or *R*) from brood year *t* was described as

$$R_t^P = \alpha^P S_t^P e^{(-\beta^P S_t^P)} e^{\in_t^P} \quad (1)$$

where α^P determined population growth at low densities, β^P represented carrying capacity for the system and $\in_t^P$ represented the error term describing deviation from expected returns (the superscript ^{P} was utilized to differentiate Pink Salmon model parameters from Coho Salmon model parameters).

We described the population dynamics of Coho Salmon with an age-stratified multistate model (Moussalli and Hilborn 1986) such that returns for brood year *t* were modeled as

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1+\left(\frac{\alpha_1}{\beta_1}+\frac{\alpha_1 \alpha_2}{\beta_2}\right) S_t} e^{\in_{t+a}} \quad (2)$$

where C_a was the proportion of Coho Salmon from brood year *t* returning at age *a*, α_1 was the per capita increase in the population at low densities in freshwater, α_2 was the per capita survival in the population

at low densities in the ocean, β_1 represented the freshwater productive capacity, β_2 represented the marine productive capacity and S_t was the number of adult spawners in year t. $\in_{t+a}$ was the error term describing deviation from expected returns and was subscripted to time $t+a$ to reference the year that Coho Salmon would return to spawn relative to brood year t. Jacks (age-.0) were ignored in this analysis because they are not properly enumerated and are estimated to comprise less than 6% of escapements (Joy and Reed 2007; Shaul et al. 2014).

The age-stratified multistate model was modified to incorporate freshwater effects related to Pink Salmon escapements, an ocean effect incorporating a shared response to ocean conditions in Coho and Pink salmon, and autocorrelation (full derivation covered in appendix 1.B). To model the freshwater effect, the freshwater productive capacity term, β_1, was linked to Pink Salmon escapements in years when juvenile Coho Salmon would be rearing (i.e., the years following brood year t). The freshwater effect was modeled as

$$F_t = f\,{S^P_{t+1}}/{\overline{S^P}} + (1-f)\,{S^P_{t+2}}/{\overline{S^P}} \tag{3}$$

where f was a number between 0 and 1 that described the relative importance of marine nutrients to young-of-the-year Coho Salmon rearing in their first summer and 1-f represented the relative importance of Pink Salmon subsidies to age-1 Coho Salmon during their second summer in freshwater. This term was calculated for each simulated year and the term γ_t was derived from the standardized version of F_t.

The ocean effect was modeled by linking the residuals from the Coho Salmon spawner-recruit models to the residuals from the Pink Salmon model. Because both Coho and Pink salmon spend one year in the ocean prior to spawning, salmon returning to spawn in a given year would have left fresh water in the same year and occupied the marine environment for the same period. If the two species demonstrated a similar response to ocean conditions, one would expect the residuals from the spawner-recruit models to be correlated. The ocean effect was modeled as the term ω_t which represented the standardized Pink Salmon error terms, $\in^P_t$ from equation (1), for each year of the simulation.

Our modified multistate model also incorporated autocorrelation and thus calculated brood year returns of Coho Salmon as

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1+\left(\frac{\alpha_1}{\beta_1+p_f\gamma_t\beta_1}+\frac{\alpha_1\alpha_2}{\beta_2}\right)S_t} e^{[(1-\phi)(p_m\omega_{t+a}+(1-p_m)\in_t^C)+\phi\in_{t+a-1}]} \quad (4)$$

where ω_t was the ocean effect (the standardized Pink Salmon error term from equation (1),$\in_t^P$) and γ_t was the freshwater effect (the standardized F_t from equation (3)). ϕ was a number between 0 and 1 that described the amount of autocorrelation present such that deviation from expected returns in year t was determined by the error in the prior year, t-1. The p_f term determined the strength of the freshwater effect (the degree to which β_1 was impacted by γ_t) such that a value of 0 would describe a system where Pink Salmon escapements had no impact on rearing Coho Salmon. Similarly, the p_m term described the strength of the ocean effect and was a value between 0 and 1 that determined the proportion of the error term associated with Pink Salmon error (ω_t). The $\in_t^C$ term represented error independent of ω_t and unique to Coho Salmon. This model was used to simulate Coho Salmon population dynamics under varying levels of freshwater effects, ocean effects, and autocorrelation (p_f, p_m and ϕ; Table 2).

Pink Salmon Simulations: North River and Ford Arm Creek Pink Salmon escapements and returns (Table 1.A.1 and 1.A.3) were fit to the Ricker model (1) and α^p and β^p were derived as the maximum likelihood estimates (Table 1.3). Expected returns were calculated from the maximum likelihood α^p and β^p estimates and equation (1). Residuals were calculated as the difference between the natural logarithms of the expected return and actual returns (Table 1.A.1 and 1.A.3).

Pink Salmon population dynamics were simulated using the Ricker model from (1) modified to include first-order autoregression such that

$$R_t^P = \alpha^P S_t^P e^{(-\beta^P S_t^P)} e^{(1-\phi^P)\in_t^P+\phi^P\in_{t-1}^P} \quad (5)$$

where ϕ^P represented the autocorrelation term specific to Pink Salmon population dynamics. ϕ^P was a number between 0 and 1 that described the amount of autocorrelation present such that the error in year t

was determined by the error in the prior year, *t-1*. Escapements, S^P, were determined by multiplying returns, R^P, by one minus the exploitation (the proportion of returns that were harvested) such that

$$S_t^P = (1 - E_t^P)R_{t-2}^P \quad (6)$$

where E_t^P was the exploitation fraction in year *t*.

To simulate 100 years of returns and escapements, the first two years of Pink Salmon escapements were seeded using two years of escapements from the original data set and returns and escapements calculated using (5) and (6). For North River simulations E_t^P was set to zero given the negligible harvest of Pink Salmon in the drainage. For each year of the Ford Arm simulations, E_t^P was randomly drawn from the exploitations calculated from the Ford Arm Pink Salmon brood table (Table 1.A.3). $\in_t^P$ values were randomly drawn from the residuals of the fitted Pink Salmon spawner-recruit model (Table 1.A.3).

Coho Salmon Simulations: Coho Salmon model parameters were derived by fitting Coho Salmon escapement and return data from the brood tables (Table 1.A.2 and Shaul et al. 2014) to the multistate model (2) and the parameters derived from the maximum likelihood estimates. Ford Arm Creek parameters were fit using the data published by Shaul et al. (2014) which included smolt abundance estimates necessary to estimate parameters associated with freshwater and marine portions of the life cycle (Table 1.3). Smolt abundance estimates were only available for two brood years of the North River Coho Salmon time series and so it was not possible to fit the multistate model to this data set.

To derive parameters for North River Coho Salmon simulations (equation 2), Coho Salmon smolt abundance was modeled using the two years of smolt abundance that were available. Coho Salmon smolt abundance for brood year 2009 and 2010 was estimated as 100,112 and 74,654 with subsequent marine survival estimates of 0.11 and 0.16 respectively (Joy et al., *unpublished data*). Marine-survival estimates for other brood years in the data series were simulated by randomly drawing numbers from a normal distribution with a mean of 0.138 and a standard deviation equal to 1.5 times the standard deviation from the two data points described above (0.0337). Smolt estimates for each brood year were generated from

the actual return estimates such that simulated smolt abundance = adult returns/simulated marine survival. We generated 250 such data sets for analysis.

Each derived data set was fit to the multistate model (2) and model parameters estimated using a maximum likelihood method. To aid the algorithm, α_1 values were constrained to be less than 500 smolts per adult spawner, marine survival was constrained to be less than 0.7, and β_2 was constrained to be between 2,000 and five times the maximum observed return for the North River (161,660). These values were considered to be well beyond the likely "true" values based on observed smolt survival from other systems (Zimmerman 2011, Shaul et al. 2014) and observed escapements (Menard et al. 2013). When the maximum likelihood algorithm produced results at these bounds the results were discarded. Maximum likelihood estimates of the parameters that did not fall at these bounds were accepted and the averages of the acceptable α_1, α_2, β_1 and β_2 estimates used in simulations (Table 3).

One hundred years of simulated Coho Salmon returns and escapements were calculated by seeding the first six years of the simulations with actual, consecutive Coho Salmon escapements taken from the original data series. Returns were calculated using (4), appropriate C_a values (Table 4) and p_f, p_m and ϕ values as prescribed for that particular simulation. γ_t and ω_t values were calculated year by year from the simulated Pink Salmon data series using (3) and (1) respectively. The f term in (3) was set to 0.5 for North River simulations and 0.7 for Ford Arm simulations based on the age distribution of the two populations (Table 4). ϵ_t^C was modeled as a random number drawn from a normal distribution with a mean of 0 and standard deviation of 0.5. Coho Salmon escapements, S_t, for years 7 to 100 were calculated from simulated returns, R_t (from 4) as

$$S_t = (1 - E_t) \sum_{a=3}^{5} C_a R_{t-a} \tag{7}$$

where E_t was the exploitation percentage. For each year of the simulation E_t was a random number drawn from a normal distribution with a mean and standard deviation equal to that estimated from the original data set (Appendix A.2 and Shaul et al. 2014).

For each combination of p_f, p_m, ϕ and ϕ^p values (Table 1.2), 500 simulations were performed. Correlations (Table 1.1) and autocorrelations were calculated from the last 15 and 25 complete years of data from each simulation (the last year in which complete returns were calculated was year 93 of the 100-year simulation). The R^2_{Adj} of the correlations was recorded as was the first and second lag autocorrelation values (Venables and Ripley 2002) for annual Pink and Coho salmon returns. To aid analysis, Coho Salmon first and second lag autocorrelations were categorized as above or below the mean. Pink Salmon first and second lag autocorrelations were categorized as less than or greater than 0.

The ability of autocorrelations to produce the five correlations (Table 1.1) in the absence of biological mechanisms was examined using the null simulations where p_f and p_m were set to zero such that no freshwater or ocean effects (and thus no interaction between Coho and Pink salmon) were present. To parse the contribution of the various types of autocorrelation on Pink-Coho correlations, generalized linear models (GLM) were fit to the null simulation results utilizing the correlation R^2_{Adj} value as the dependent variable and the four autocorrelations measured (Pink and Coho salmon first and second lag autocorrelations) as the independent variables, including all two-way interaction terms. GLM estimates were examined for the strength of the relationship between autocorrelation strength and correlation R^2_{Adj} values.

To determine how freshwater effects, ocean effects and autocorrelation manifested as the correlations in Table 1.1, simulation results were examined using smoothed contour plots of the correlation R^2_{Adj} values as a function of freshwater effect size (p_f) and ocean effect size (p_m) for each combination of Coho and Pink salmon first lag autocorrelation categories. To determine how correlations produced in the original brood tables aligned with simulated results we compared correlation R^2_{Adj} values from the original brood tables to those produced by simulations with similar Pink and Coho salmon first lag autocorrelations. The Norton Sound composite and the Kwiniuk, Niukluk and Nome river brood tables were compared to North River simulations given the similar life history (age distribution; Table 1.4) of Coho Salmon in the region.

Results

Autocorrelation and the frequency of Coho – Pink salmon correlations in the absence of biological effects: As predicted, in the absence of any biological effect (null simulations where freshwater, p_f, and ocean effect sizes, p_m, were set to 0), autocorrelation produced significant correlations between Coho and Pink salmon more frequently than would be expected by random chance. More specifically, it was high levels of autocorrelation at multiple lags for one or both species that resulted in cross-species correlations being produced and GLM estimates in excess of 0.10. GLM estimates of individual autocorrelations were modest (<0.05) in all but two instances and in some cases, interactions between autocorrelations produced GLM estimates upwards of 0.40 (Table 1.5). The $Return_1$ and $Return_{12}$ correlations were the most likely to arise from autocorrelative processes alone and interactions between autocorrelations produced GLM estimates of up to 0.40 (Table 1.5). *Marine* correlations were produced similarly by autocorrelation, but were much less sensitive, and interactions between autocorrelations produced GLM estimates of up to 0.11. The *Prod* correlations were the least likely to be produced by autocorrelative processes, and interactions between autocorrelations produced GLM estimates that never exceeded 0.10.

Strength of Return, Prod and Marine correlations in relation to freshwater and ocean effects: The *Return* correlations, relating brood year returns of Coho Salmon to Pink Salmon escapements during Coho Salmon freshwater rearing years, were consistently produced by large freshwater effects (p_f values) simulating an MDN benefit of Pink Salmon on Coho Salmon (Figure 1.2). This pattern was consistent for both correlations and at all first lag autocorrelation categories, although correlation strength was positively related to the strength of the autocorrelation (Figure 1.2). $Return_1$ correlations were also weak and less frequent when Pink Salmon exhibited even year dominance (first lag autocorrelation < 0) (Figure 1.2). In the Ford Arm simulations, $Return_{12}$ correlations were stronger and more likely in conjunction with a moderate, correlated response of the two species to marine conditions (ocean effects).

Sizable $Return_{12}$ correlations were present in all the examined brood tables which indicated strong freshwater and minimal ocean effects in the simulations (Figure 1.2 and Table 1.C.1). Strong $Return_1$

correlations were only present in the Ford Arm and North River data series. Both data series had $Return_1$ R^2_{Adj} values greater than those produced by simulations with similar autocorrelative values, indicating freshwater effects. Brood tables that exhibited even year dominance in Pink Salmon returns (Norton Sound Composite and Kwiniuk, Nome and Niukluk rivers) did not produce $Return_1$ correlations. We considered these results uninformative given that $Return_1$ correlations were uncommon and small when first lag Pink Salmon autocorrelations were negative.

The *Prod* correlations, relating Coho Salmon productivity (returns-per-spawner) to Pink Salmon escapements during Coho Salmon freshwater rearing years, were much weaker, less likely to occur, and their relationship to biological effects varied based on the stock simulated and the amount of autocorrelation present. In the Ford Arm simulations, with the younger age distribution (Table 1.4), the *Prod* correlations were only produced by large freshwater effects and minimal ocean effects (Figure 1.3). However, for the North River simulations and the older age distribution, the amount of autocorrelation in Pink and Coho salmon data series greatly affected whether ocean or freshwater effects were more likely to produce *Prod* correlations (Figure 1.3). With negative Pink Salmon first-lag autocorrelations, the $Prod_1$ correlation was weak and rarely produced, while the $Prod_{12}$ correlation was most often produced by large freshwater effects and minimal ocean effects. However, with positive Pink Salmon first-lag autocorrelations, the *Prod* correlations were most often produced by large ocean effects and small freshwater effects *or* minimal ocean effects combined with large freshwater effects (Figure 1.3).

The only brood table with a notable $Prod_1$ correlation was the Ford Arm data series, indicating freshwater effects (Figure 1.3 and Table 1.C.1). The $Prod_1$ correlation was absent or minimal in the Norton Sound brood tables, an uninformative result given how the $Prod_1$ correlation was not clearly indicative of any effect in North River simulations. The North River brood table produced a $Prod_1$ R^2_{Adj} value that indicated one of two possibilities; either strong marine and minimal freshwater effects *or* strong freshwater and minimal ocean effects. The Norton Sound brood tables with even year dominance in Pink

Salmon escapements (the Kwiniuk, Niukluk, Nome Rivers and the Norton Sound composite) produced negative R^2_{Adj} values.

The $Prod_{12}$ correlation was present to variable degrees in real brood tables and was indicative of strong freshwater effects in most cases (Figure 1.3 and Table 1.C.1). However, in the case of the North and Nome rivers the $Prod_{12}$ correlation may have indicated sizable ocean effects as well (Figure 1.3). The Ford Arm, Kwiniuk River, Niukluk River and Norton Sound composite brood table produced $Prod_{12}$ R^2_{Adj} values that indicated freshwater effects in simulations with similar autocorrelation values. The North River brood table, with its high first lag autocorrelation in Pink and Coho salmon returns, produced a sizable $Prod_{12}$ R^2_{Adj} value that indicated either a strong marine and minimal freshwater effect *or* a strong freshwater and minimal ocean effect. The Nome River brood table produced a negative $Prod_{12}$ R^2_{Adj} value that indicated large freshwater *and* ocean effects.

Marine correlations, relating annual escapements of the two species, were readily produced in both simulations when both species responded similarly to ocean conditions (ocean effects, p_m). For North River simulations, the correlation was slightly more likely when strong freshwater effects combined with ocean effects, but was unrelated to freshwater effects in Ford Arm simulations (Figure 1.4). Increasing autocorrelation in Pink Salmon returns increased the likelihood and strength of *Marine* correlations while increasing levels of Coho Salmon autocorrelation reduced the probability of observing the *Marine* correlation (Figure 4). The *Marine* R^2_{Adj} values present in the brood tables were modest relative to those produced in the simulations and indicated a small to moderate ocean effects (Figure 1.4 and Table 1.C.1).

Discussion

Strong freshwater effects, manifesting as Coho Salmon responses to Pink Salmon MDN, were consistently the most likely generator of observed patterns in the data series examined, even though which correlations were detected varied among systems. While outside the bounds of traditional statistical

testing, our approach provided valuable insight into the most likely explanation for observed patterns, even with the relatively short term data series examined. We demonstrated that simultaneously examining multiple hypotheses while accounting for autocorrelation formed a stronger basis for inferences about the relationship between Coho and Pink salmon populations, given multiple conflatin factors (i.e, different life histories of the two species, multiple correlations relating their population dynamics and autocorrelative processes inherent in the data sets).

Evidence of biological effects: Our results support the hypothesis that Coho Salmon populations respond favorably to MDN contributed to freshwater systems by Pink Salmon. Examining correlative patterns while accounting for autocorrelation consistently indicated that MDN from spawning Pink Salmon was the most likely explanation for observed patterns linking Coho and Pink salmon, even though each brood table exhibited unique patterns. Furthermore, the correlations measured in the brood tables were quite strong with R^2_{Adj} values often in excess of 0.50 and as high as 0.76. Correlations of that strength were unlikely to be produced by autocorrelation alone and were actually rare occurrences in our simulations, regardless of freshwater and ocean effect sizes.

Our results match the population-level effects inferred from previous smaller scale MDN studies and inform our understanding of how escapement estimates translate to an MDN benefit from one species to another. MDN from Pink Salmon can affect the growth (Wipfli et al. 2003; 2010), lipid content (Heintz et al. 2004, 2010) and local abundance (Nelson and Reynolds 2014) of juvenile Coho Salmon. Our results suggest that these benefits propagate from individuals to populations, thus affecting stock-level Coho Salmon dynamics. Research conducted at the population level on lake rearing Sockeye Salmon has produced sometimes inconclusive results (Schindler et al. 2005; Uchiyama et al. 2008; Adkison 2010), while population scale studies on stream rearing salmonids such as Coho and Chinook (*O. tshawytscha*) salmon have been rare. This study helps fill a gap in our understanding of how escapement estimates can be interpreted from an MDN perspective and ultimately influence salmon productivity (Piccolo et al. 2009).

Our results align well with other studies in which both Coho Salmon smolt and adult data are available, thus providing additional support of MDN effects. In Ford Arm Creek, Shaul et al. (2014) demonstrated that Coho Salmon adult returns and smolt abundance were better predicted by Pink Salmon abundance than by the number of spawning Coho Salmon. Our results are consistent with their findings, as we demonstrated that freshwater effects were the best explanation for the similar trends in abundance of Pink and Coho salmon in their data. Results from the Norton Sound systems were less striking than Ford Arm results, which was expected given the shorter data series. The shorter data series made the production of the various correlations in the absence of biological effects more likely, as autocorrelated trends would need fewer years to produce spurious results. The North River data series was particularly ambiguous given the high first and second lag autocorrelations seen in both Coho and Pink salmon in this data series. Nevertheless, the consistency of the Norton Sound results and the agreement between our Ford Arm simulations and Shaul et al. (2014) analysis supports our conclusions.

Our results also align with research in Washington state (Michael 1995 and Zimmerman 2011) and demonstrate how differing age structure in Coho Salmon throughout their range may affect correlative patterns in the two species. A correlation similar to $Prod_1$ was first documented in the Skagit River (Michael 1995) and a correlation between Coho Salmon smolt production and Pink Salmon abundance during Coho Salmon rearing years has since been documented in the Skagit River (Zimmerman 2011) providing additional evidence of a marine-subsidy effect. Throughout their range Coho Salmon spend one year in the ocean after one to three years in freshwater. The Skagit River is dominated by 3-year-old adults (fish that spend only one year in fresh water), while The Ford Arm stock has a more even balance between 3- and 4-year-old adults and Norton Sound is dominated by 4-year-old adults (fish that spend two years in freshwater) (Table 1.4). The *Prod* correlations were produced by both ocean and freshwater effects in the North River simulations, but were produced by freshwater effects in the Ford Arm simulations. The differing results were likely the product of variable age structure in the two Coho Salmon populations due to how the different aged Coho Salmon populations align with Pink Salmon

populations. While the *Prod* correlations appeared to be a useful indicator of freshwater effects with the younger age distribution, it was clear that these correlations could indicate very different relationships with the older age distribution, dependent on the amount of autocorrelation.

Agreements between this study, Ford Arm Creek studies (Shaul et al. 2014) and Pacific Northwest studies (Michael 1995; Zimmerman 2011) demonstrate that these coupled Pink-Coho salmon dynamics are likely present throughout the range of the two species, suggesting that wherever these two species overlap in time and space MDN effects may be present. It should be noted that the correlative patterns we examined were not always produced in simulations even when freshwater effects were present in the simulation model due to random variability outweighing smaller effect sizes. Thus, the absence of these correlations in other data sets does not necessarily preclude the presence of such effects and of course highlights the importance of generating long term data series to detect subtler relationships.

Correlations as strong as those present in brood tables were rare in our simulations, suggesting that our multistate model may have underestimated the effect of Pink Salmon MDN on Coho Salmon productivity. Coho Salmon smolts have been documented as significant predators on Pink Salmon smolt both in fresh water and the ocean (Joy Dissertation Chapter 2, Williams et al. 2009, Hargreaves and LeBrasseur 1985), and smolt body size have demonstrated a positive response to MDN in the Unalakleet (Joy et al. *in prep*[a]) and Nome river watersheds (Williams et al. 2009). Smolt body size is correlated with marine survival (Holtby et al. 1990; Beamish et al. 2004; Duffy and Beauchamp 2011), suggesting that in addition to modeling freshwater capacity, β_1, as a function of Pink Salmon escapements, we also could have modeled marine survival, α_2, as a function of Pink Salmon escapements (Even though we are referring to marine survival, linking the α_2 term to Pink Salmon escapements in the years' after the Coho Salmon parent generation spawned, (γ_t) still describes the freshwater effect; see equation 3 and 4). Linking marine survival to Pink Salmon escapements would certainly increase both the strength and frequency of *Return* and *Prod* correlations. Furthermore, modeling the effects of Pink Salmon escapement on freshwater capacity assumes density dependence in Coho Salmon. However, Coho

Salmon productivity is thought to be a function of freshwater habitat quality and quantity and is often modeled with a "bent hockey-stick" model (Bradford et al. 1997, 2000; Shaul et al. 2014). This model assumes a proportionate, density-independent response to Coho Salmon spawner abundance at low escapements that transitions to a constant return (independent of escapements and hence density) at a fixed reference point determined by habitat quality and quantity. Linking that reference point to Pink Salmon escapements (Shaul et al. 2014) would certainly produce correlations with greater strength and frequency than were produced by our models.

Support for a similar response to ocean conditions in the two salmon species (ocean effects) was much weaker than that for freshwater effects, but results suggested a small degree of a correlated response by the two species. Salmon species have demonstrated similar trends in abundance at both regional (Pyper et al. 2005) and ocean-basin scales (Stachura et al. 2014) and furthermore, evidence from Southeast Alaska demonstrates that Pink Salmon smolt act as a predator buffer for Coho Salmon smolt such that higher Pink Salmon smolt abundance increases Coho Salmon smolt survival (LaCroix et al. 2009). On a broader scale, harvests of Coho and Pink salmon over more than 50 years in Southeast Alaska were strongly correlated, suggesting a correlated response of the two species to ocean conditions in that region (Shaul et al. 2007). Similarly, the Norton Sound composite data series suggested small ocean effects that were stronger than in the individual Norton Sound systems (Figure 1.4). Ocean effects are probably manifested at relatively broad scales rather than finer, stock-level (i.e., watershed) scales. In the cases when smaller stocks do not demonstrate strong ocean effects, these marine drivers may be obscured by other, relatively strong drivers acting on individual stocks, such as freshwater/marine-subsidy effects. A similar response to ocean conditions by two different species could result from a number of causes such as an overlap in oceanic distribution (Weitkamp et al. 2011) or the predator buffering mechanism (LaCroix et al. 2009). In the case of Coho and Pink salmon, the former has been shown to prey on the latter both during the freshwater phase of the smolt migration (which would produce a freshwater effect; Joy et al. *in prep*[b]) and in the marine environment (which would produce a marine effect; Hargreaves and LeBrasseur 1985), thus

correlating their abundances. Furthermore, environmental variables including those associated with the Pacific Decadal Oscillation (PDO) and sea surface temperature likely contribute to covariation in Pacific salmon (Mantua et al. 1997; Hare et al. 1999).

One aspect of marine interactions that we did not explore involves potential competition between Pink and Coho salmon. In Southeast Alaska there has been a strong biennial pattern whereby the weight of adult Coho Salmon is inversely related to Pink Salmon biomass with subsequent impact on late-ocean, growth-related mortality (Shaul and Geiger 2016). These negative correlations could have a dampening influence on the positive relationships we examined in this paper. Furthermore, in addition to affecting survival, the reduction in Coho Salmon weights was most pronounced in females and the authors of the study suggest that effects would cascade forward with reduced fecundity (Shaul and Geiger 2016). Incorporating these effects into our simulations could be informative but would also add another layer of complexity to what we have tried to untangle here, particularly if we modelled the lagged effect of reduced fecundity. A negative correlation in adult returns should demonstrate similar patterns to our *marine* correlations but with negative correlations instead of positive (but similar R^2_{Adj}values). However, the interaction of negative ocean effects with freshwater effects is not immediately clear, and would likely require further simulations to disentangle.

Autocorrelation: Long-term trends in salmon population time series are common and characterized by high autocorrelations at several lags making correlative analysis inherently flawed (Pyper and Peterman 1998). Multiple corrections have been suggested for this issue (Pyper and Peterman 1998) and more complex modeling systems, such as dynamic factor analysis (DFA), have been derived to deal with autocorrelation in time series (Zuur et al. 2003; Stachura et al. 2014). These techniques are still sensitive to sample size considerations and Zuur et al. (2003) recommend using other techniques in conjunction with DFA. We believe our approach provides another useful tool for examining similar trends in species abundance and allows comparisons of likely explanations even when time series are relatively short. Using simulations, we were able to examine how these correlative patterns arose as a function of

autocorrelation on its own and, more importantly, how autocorrelation interacted with biological effects to dampen or increase the likelihood of such patterns arising.

Other considerations and caveats: As with all modeling exercises there are potential pitfalls. All models are by definition wrong to some extent; they are simplified, mathematical constructs meant to imitate complex systems. Model choice and over-simplification may be faulty and escapement and harvest data can have considerable error. This simulation exercise could be expanded to include measurement error as a variable, although the models would likely become unwieldly and incorporating measurement error would reduce the probability of detecting significant correlations even when effects were present. Despite potential flaws, it is important to remember that the correlations examined here are best thought of as broad patterns present in the data and despite obvious error at all levels, describe similar trends in the two species.

Management implications: Incorporating MDN effects into management has been difficult because the response of salmon populations to MDN from escapements, as measured by management agencies, is not well understood (Piccolo et al. 2009). This study helps to address this knowledge gap. While it may be premature to incorporate Pink Salmon into forecasting and management of Coho Salmon in the Norton Sound region, the evidence provided here and the studies cited in this paper lend credence to exploring multi-species management models. If these patterns continue in the coming decade, it may be prudent to adopt an approach similar to that taken in Washington State (Zimmerman 2011) and Ford Arm Creek (Shaul et al. 2014) where Pink Salmon escapements are used to aid Coho Salmon forecasts. Furthermore, re-examining escapement goals in light of these interactions would be worthwhile.

From a spawner biomass standpoint, the two systems simulated in this study are both dominated by Pink Salmon. However, Pink Salmon are not the only salmon species providing marine nutrients to freshwater systems and in some years may not be the most dominant. Chum and Sockeye salmon provide similar loads of nutrients to other systems, but due to their different life histories (including differing age structures in both fresh and salt water), correlations between these species and Coho Salmon would likely

manifest differently from Pink-Coho salmon relationships. Furthermore, the response of juvenile stream-type Chinook Salmon (which rear for one year in freshwater) to MDN is as strong as that of Coho Salmon (Joy et al. *in prep*[a]) and spawning Chinook Salmon, which can migrate thousands of kilometers up rivers (Brown et al. 2017), contribute MDN to systems that also affects juvenile salmon rearing in freshwater (Joy et al *in prep*[b]). A similar approach to that taken here may be useful for understanding how relationships between other salmon species would produce similar trends in population dynamics.

These results also present a framework for biologists in other regions where Pink and Coho salmon overlap in distribution to examine their data for potential interactions. Unfortunately, quality escapement estimates of Coho and Pink salmon tend to be limited in Alaska given the late run timing and moderate harvest pressures of the former, and the extensive use of aerial counts to monitor the latter. While escapement monitoring occurs with the current goal of managing salmon in single-species spawner-recruit frameworks, this study demonstrated the utility of monitoring all salmon species in a system. Furthermore, obtaining smolt data would allow easier disentanglement of freshwater and ocean effects than the exercise undertaken here. Pacific salmon species have the potential to interact with each other through a variety of mechanisms including predation, marine subsidies, and competition, and furthermore may respond similarly to environmental conditions. Monitoring escapements, as well as developing smolt monitoring programs, of all salmon species has the potential to elucidate these interactions which may ultimately aid managers in sustaining healthy fish populations and fisheries.

Conclusions: The goal of this study was to determine the most likely explanation for observed correlative patterns, even with limited data series. Our simulations produced consistent results across Norton Sound systems and with Ford Arm Creek. Conclusions from the Ford Arm system are supported by Shaul et al. (2014) and our analysis meshes nicely with Skagit River studies (Michael 1995; Zimmerman 2011), which legitimized our approach and conclusions and demonstrated that these relationships exist throughout the range of the two species. Finally, our results agree with expectations from smaller scale studies on Pink Salmon MDN effects on Coho Salmon. Thus, despite small sample sizes, this study

provides compelling evidence that MDN from Pink Salmon is an important driver of Coho Salmon productivity in these systems.

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References

Adkison, M. A. 2010. Models of the effects of marine-derived nutrients on salmon (*Onchorhynchus* spp.) population dynamics. Can. J. Fish. Aquat. Sci. 67: 5-15.

Beamish, R. J., C. Mahnken and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Trans. Am. Fish. Soc. 133: 26-33.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. 2, vol. 19. U.K. Ministry of Agriculture, Food and Fisheries, London.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. 53: 164-173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Can. J. Fish. Aquat. Sci. 55:1909-1918.

Bradford, M. J., R. A. Myers, and J. R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Can. J. Fish. Aquat. Sci. 57: 677-686.

Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Am. Fish. Soc. 126: 49-64.

Brown, R. J., R. J. Henszey, A. von Finster, and J. H. Eiler. 2017. Catalog of Chinook Salmon spawning areas in the Yukon River basin in Canada and the United States. J Fish Wildl Manag.8: 558-587.

Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Can. J. Fish. Aquat. Sci. 68: 232-240.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24: 6-14.

Hargreaves, N. B. and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Can. J. Fish. Aquat. Sci. 42: 659-668.

Haught, S. B., R. E. Brenner, J. W. Erickson, J. W. Savereide, and T. R. McKinley. 2017. Escapement goal review of Copper and Bering rivers, and Prince William Sound Pacific salmon stocks, 2017. Alaska Department of Fish and Game, Fishery Manuscript No. 17-10, Anchorage.

Heintz, R. A., B. D. Nelson, J. Hudson, M. Larson, L. Holland, and M.S. Wipfli. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Trans. Am. Fish. Soc. 133: 559-567.

Heintz, R. A., M. S. Wipfli, and J. P. Hudson. 2010. Identification of marine-derived lipids in juvenile coho salmon and aquatic insects through fatty acid analysis. Trans. of the Am. Fish. 139: 840-854.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47: 2181-2194.

Jones, E. L., T. J. Quinn, and B. W. Van Alen. 1998. Observer Accuracy and Precision in Aerial and Foot Survey Counts of Pink Salmon in a Southeast Alaska Stream. N. Am. J. Fish. Manag. 18(4):832–846.

Joy, P. J., C. S. Stricker, W. Jones, S. Y. Wang, J. Huang, M. Tyers, A.C. Seitz, and M. S. Wipfli. *In prep*[a]. Marine nutrients and subsidies linked to watershed-scale salmon spawner abundance estimates (escapements) increase growth, size and condition of juvenile Coho and Chinook salmon.

Joy, P. J., C. S. Stricker, W. Jones, M. Tyers, A.C. Seitz, and M. S. Wipfli. *In prep*[b]. Bridging the gap between salmon spawner abundance and marine nutrient use by juvenile salmon: seasonal cycles and landscape effects at the watershed scale.

Joy, P. and D. J. Reed. 2007. Estimation of coho salmon abundance and spawning distribution in the Unalakleet River 2004 - 2006. Alaska Department of Fish and Game, Fishery Data Series No. 07-48, Anchorage.

LaCroix, J. J., A. C. Wertheimer, J. A. Orsi, M. V. Sturdevant, E. A. Fergusson, and N. A. Bond. 2009. A top-down survival mechanism during early marine residency explains coho salmon year-class strength in southeast Alaska. Deep-Sea Research Part II: Topical Studies in Oceanography 56(24):2560–2569.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. B. Am. Meteorol. Soc. 78: 1069-1079.

Menard, J., J. Soong, S. Kent, and A. Brown. 2013. 2012 Annual management report Norton Sound – Port Clarence Area, and Arctic-Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 13-28, Anchorage.

Michael Jr., J. H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Science, 69: 228-233.

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Can . J. Fish. Aquat. Sci. 43: 135-141.

Needle, C. L. 2002. Recruitment models: diagnosis and prognosis. Rev. Fish Biol. And Fish. 11: 95-111.

Nelson, M. C. and J. D. Reynolds. 2014. Time-delayed subsidies: interspecies population effects in salmon. PLoS ONE 9(6): e98951.

Neter, J., M. H. Kutner, C. J. Nachtsheim and W. Wasserman. 1996. Applied Linear Statistical Models (4th Ed.)Irwin Publishing, Chicago, IL.

Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. 55: 2503-2517.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Linking Alaskan salmon fisheries management with ecosystem-based escapement goals: a review and prospectus. Fisheries 34: 124-134.

Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of northeast Pacific salmon. Trans. Am. Fish. Soc. 134: 86-104.

Pyper, B. J. and R. M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analysis of fish data. Can. J. Fish. Aquat. Sci. 55:2127-2140.

Quinn, T. R. II and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Canada, Bull. No. 191.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology, 86 (12), 3225-3231.

Shaul, L. D., and H. J. Geiger. 2016. Effects of climate and competition for offshore prey on growth, survival, and reproductive potential of Coho Salmon in Southeast Alaska. North Pacific Anadromous Fish Commission Bulletin 6: 329-347.

Shaul, L. D., K. F. Crabtree, K. C. Koolmo, K. M. Koolmo, J. V. Nichols, and H. J. Geiger. 2014. Studies of coho salmon and other *Oncorhynchus* species at Ford Arm Creek, 1982 – 2009. Alaska Department of Fish and Game, Fishery Manuscript Series No. 14-02, Anchorage.

Shaul, L., L. Weitkamp, K. Simpson and J. Sawada. 2007. Trends in abundance and size of coho salmon in the Pacific rim. N. Pacific Anadromous Fish Commision 4: 93-104.

Soong, J., A. Banducci, S. Kent, and J. Menard. 2008. 2007 annual management report Norton Sound, Port Clarence, and Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 08-39, Anchorage.

Stachura, M. M., N. J. Mantua, and M. D. Scheuerell. 2014. Oceanographic influences on patterns in North Pacific salmon abundance. Can. J. Fish. Aquat. Sci. 71: 226-235.

Uchiyama, T., B. P. Finney, and M. D. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Onchorhynchus nerka*). Can . J. Fish. Aquat. Sci. 65: 1635-1648.

Venables, W. N. and Ripley, B. D. (2002) *Modern Applied Statistics with S.* Fourth Edition. Springer-Verlag.

Weitkamp, L. A., J. A. Orsi, K. W. Myers and R. C. Fransis. 2011. Contrasting early marine ecology of Chinook salmon and coho salmon in Southeast Alaska: insight into factors affecting marine survival. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science 3: 233-249.

Williams, B. C., M. J. Nemeth, R. C. Bocking, C. Lean, and S. Kinneen. 2009. Abundance and marine survival of coho salmon smolts from the Nome River, Alaska, 2006-2008. Report prepared for the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative by LGL Alaska Research Associates, Inc. and Norton Sound Economic Development Corporation. 41 p. + appendices.

Wipfli, M. S., J. P. Hudson, J. P. Caouette and N. L. Mitchell. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic lveles in streamside experimental channels. Trans. Am. Fish. Soc. 139: 824-839.

Wipfli, M. S., J. Hudson, D. T. Chaloner and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Can. J. Fish. Aquat. Sci. 56: 1600-1611.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Trans. Am. Fish. Soc. 132: 371-381.

Zabel, R. W. and P. S. Levin. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia 133: 349-355.

Zimmerman, M. 2011. 2011 wild coho forecasts for Puget Sound, Washington Coast, and Lower Columbia. Washington Department of Fish and Wildlife, Olympia, Washington.

Zuur, A. F., I. D. Tuck, and N. Bailey. 2003. Dynamic factor analysis to estimate common trends in fisheries time series. Can. J. Fish. Aquat. Sci. 60: 542-552.

Table 1.1. Correlations between Coho and Pink salmon examined in brood tables and measured in simulations. R_t denotes total returns and S_t denotes the number of spawners (escapement) in year t.

Correlation Name	Dependent Variable (Coho)	Independent Variable(s) (Pink)
$Return_1$	R_t	S^P_{t+1}
$Return_{12}$	R_t	$S^P_{t+1} + S^P_{t+2}$
$Prod_1$	R/S_t	S^P_{t+1}
$Prod_{12}$	R/S_t	$S^P_{t+1} + S^P_{t+2}$
Marine	S_t	S^P_t

Table 1.2. Range of freshwater effects (p_f), ocean effects (p_m), and autocorrelation (ϕ and ϕ^p) values used in simulations of North River and Ford Arm stocks.

Stock	***Freshwater Effect*** p_f	***Ocean Effect*** p_m	***Coho Autocorrelation*** ϕ	***Pink Autocorrelation*** ϕ^p
North River	0 – 0.7 by 0.1 increments	0 – 1.0 by 0.2 increments	0 - 0.75 by 0.25 increments	0 - 0.9 by 0.3 increments
Ford Arm	0 – 0.3 by 0.05 increments	0 – 1.0 by 0.2 increments	0 - 0.75 by 0.25 increments	0 - 0.75 by 0.25 increments

Table 1.3. Maximum likelihood estimates of spawner-recruit model parameters fit to original brood tables and used in simulations.

Species	Stock	Model	α		β	
			α_1	α_2	β_1	β_2
Pink	North	Ricker	1.381		9.14×10^{-7}	
	Ford Arm		2.744		2.02×10^{-6}	
Coho	North[a]	Multistate	75.17 (65.89)	0.197 (0.029)	146,620 (47,325)	60,014 (30,926)
	Ford Arm		161.41	0.14	77,781	75,153

[a] North River Coho Salmon parameters represent the average (and standard deviation) of the 173 simulated parameter estimates that were considered acceptable for analysis.

Table 1.4. Age structure used for Coho Salmon simulations.

Stock	Age Proportion, C_a		
	$a = 3$	$a=4$	$a=5$
North River[a]	0.11	0.81	0.08
Ford Arm Cr.[b]	0.58	0.41	0.01

[a]Soong et al. 2008
[b]Shaul et al. 2014

Table 1.5. General linear model results for each correlation R^2_{Adj} value as a function of first and second lag autocorrelation in Pink and Coho salmon returns (including interactions) from North River 15 year and Ford Arm 25-year null simulations. Bold denotes significance at alpha = 0.05.

Autocorrelation	*Correlation*	*North*		*Ford Arm*		*Correlation*	*North*		*Ford Arm*	
		Est	**P-value**	**Est**	**P-value**		**Est**	**P-value**	**Est**	**P-value**
Coho 1st Lag		-0.01	0.58	0.02	**0.08**		0.01	0.19	0.01	0.33
Pink 1st Lag		**0.02**	**0.05**	0.02	0.19		**0.03**	**0.00**	0.00	0.76
Coho 2nd Lag		**-0.02**	**0.04**	0.00	0.77		0.00	1.00	-0.02	0.13
Pink 2nd Lag		0.00	0.72	**0.07**	**0.00**		0.00	0.76	0.01	0.64
Co 1st x Co 2nd	*Return*$_1$	**0.13**	**0.00**	-0.01	0.68	*Prod*$_1$	**0.05**	**0.02**	0.01	0.49
Co 1st x Pi 1st		**0.18**	**<0.01**	0.02	0.58		**0.09**	**0.00**	0.03	0.34
Co 1st x Pi 2nd		**0.07**	**0.01**	**-0.13**	**0.01**		-0.02	0.40	-0.03	0.47
Pi 1st x Co 2nd		**0.10**	**0.00**	0.04	0.07		0.02	0.21	-0.01	0.81
Co 2nd x Pi 2nd		**0.20**	**0.00**	**0.18**	**0.00**		**0.06**	**0.02**	**0.07**	**0.02**
Pi 1st x Pi 2nd		0.01	0.49	0.01	0.37		**-0.04**	**0.01**	-0.02	0.09
Coho 1st Lag		-0.01	0.61	0.02	0.26		**0.03**	**0.07**	0.02	0.29
Pink 1st Lag		**0.04**	**0.00**	0.04	0.17		**0.04**	**0.00**	0.02	0.28
Coho 2nd Lag		0.00	0.85	-0.02	0.36		0.01	0.51	-0.01	0.41
Pink 2nd Lag		0.02	0.27	0.08	**0.01**		-0.02	0.27	0.01	0.73
Co 1st x Co 2nd	*Return*$_{12}$	**0.09**	**0.01**	0.02	0.45	*Prod*$_{12}$	**0.05**	**0.10**	0.00	0.86
Co 1st x Pi 1st		**0.14**	**0.00**	0.01	0.87		**0.06**	**0.00**	-0.01	0.86
Co 1st x Pi 2nd		**0.11**	**0.01**	**-0.13**	**0.06**		0.01	0.87	-0.03	0.64
Pi 1st x Co 2nd		**0.08**	**0.00**	0.03	0.40		0.03	0.20	0.02	0.61
Co 2nd x Pi 2nd		**0.40**	**<0.01**	**0.29**	**0.00**		**0.09**	**0.02**	**0.08**	**0.06**
Pi 1st x Pi 2nd		**-0.04**	**0.09**	-0.02	0.18		**-0.05**	**0.01**	**-0.03**	**0.02**
Coho 1st Lag		**0.02**	**0.06**	**0.02**	**0.09**					
Pink 1st Lag		0.00	0.80	-0.02	0.16					
Coho 2nd Lag	*Marine*	0.00	0.74	**-0.03**	**0.01**					
Pink 2nd Lag		**0.03**	**0.00**	0.04	0.06					
Co 1st x Co 2nd		0.02	0.40	**0.05**	**0.01**					
Co 1st x Pi 1st		**0.11**	**0.00**	**0.08**	**0.01**					

Co 1st x Pi 2nd	-0.04	0.16	**-0.08**	**0.06**
Pi 1st x Co 2nd	**0.03**	**0.05**	-0.01	0.80
Co 2nd x Pi 2nd	**0.10**	**0.00**	**0.09**	**0.00**
Pi 1st x Pi 2nd	0.02	0.25	0.00	0.86

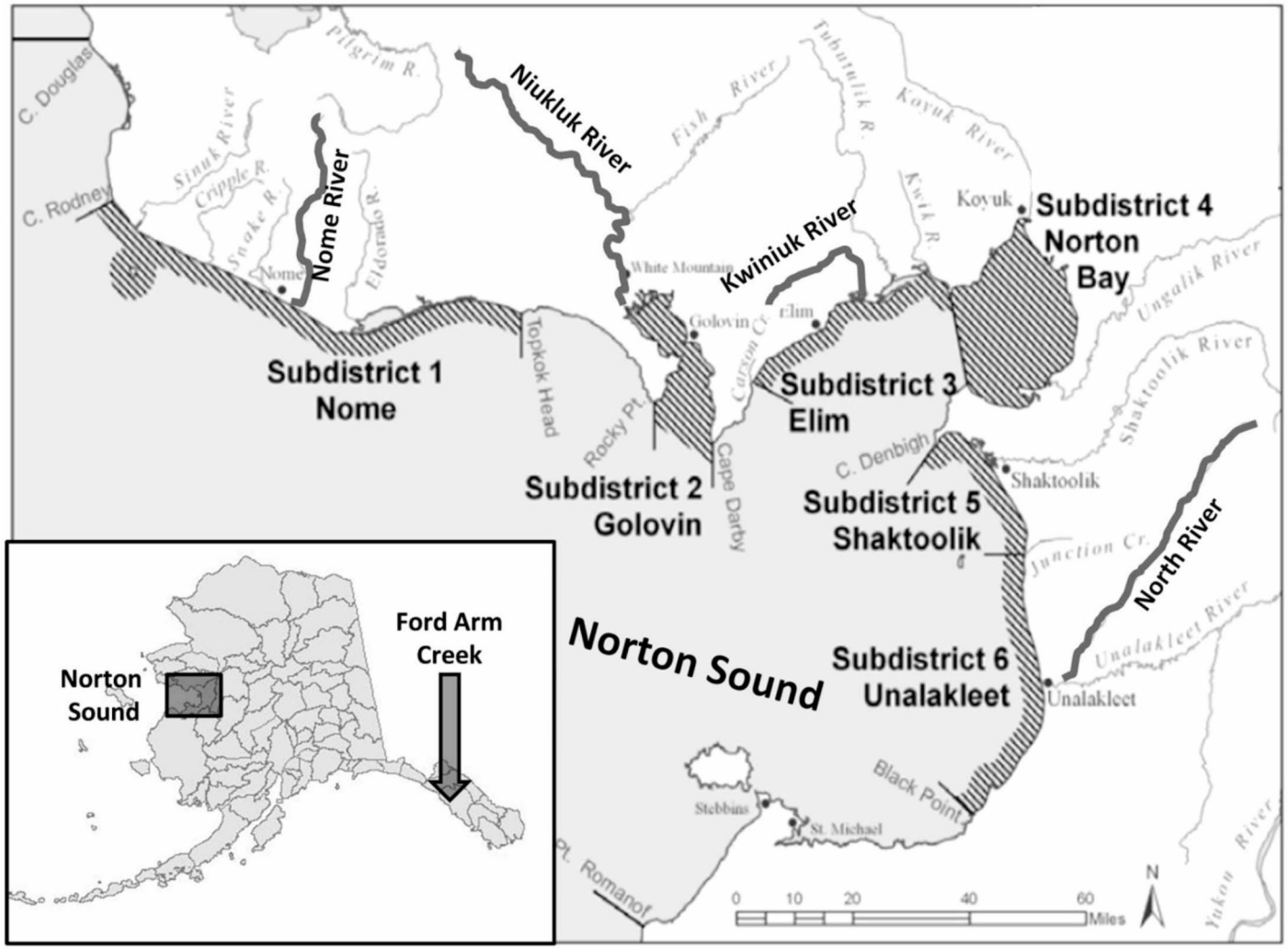

Fig 1.1. Map displaying Norton Sound, the North, Kwiniuk, Niukluk and North rivers and the Norton Sound commercial salmon fishing subdistricts (Menard et al. 2013) and the location of Ford Arm Creek in Southeast Alaska.

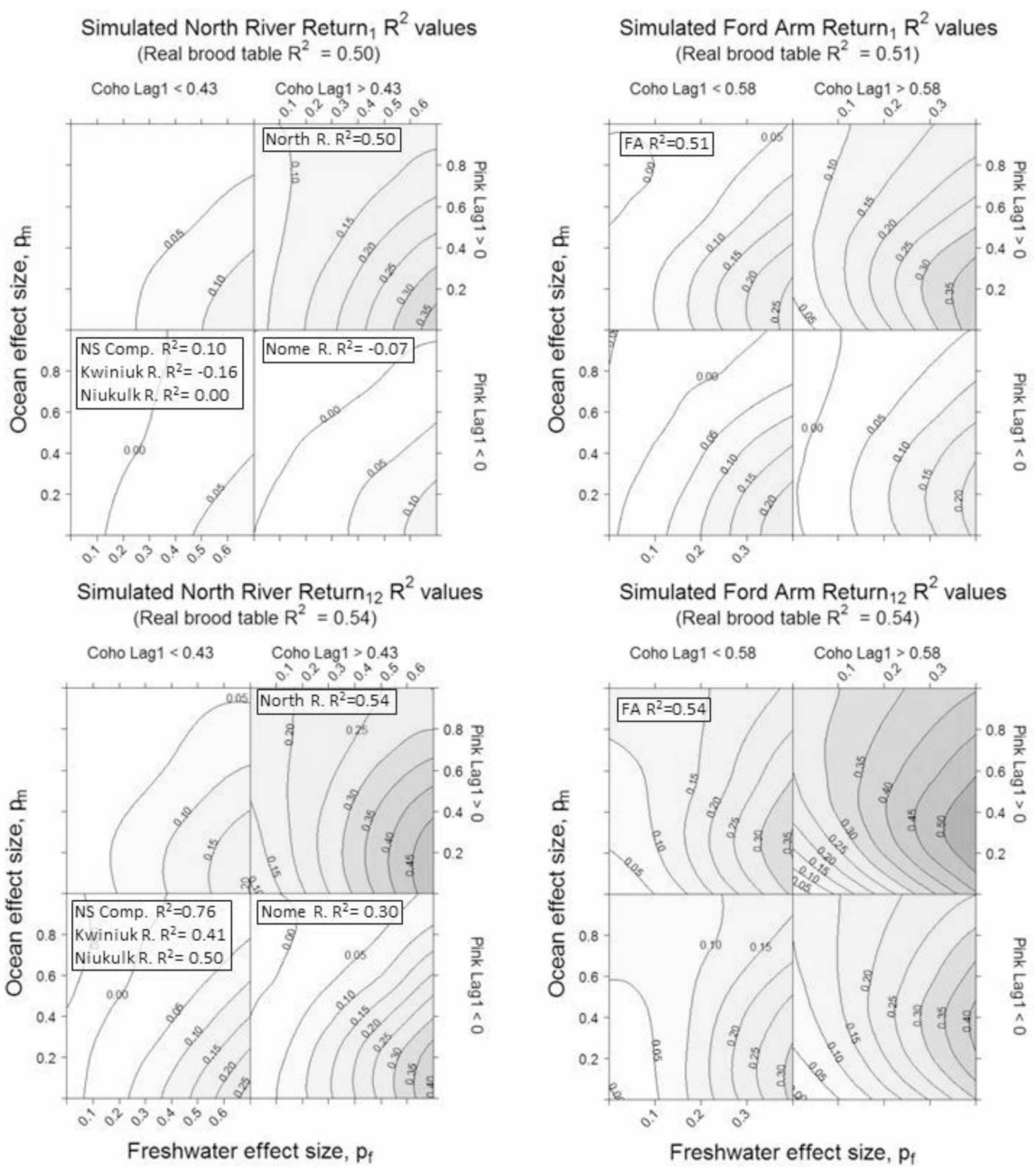

Fig 1.2. Smoothed contour plots of the average R^2_{Adj}values of *Return*$_1$ (top row) and *Return*$_{12}$ (bottom row) correlations as a function of freshwater (p_f) and ocean effect (p_m) sizes for each combination of Coho and Pink salmon first lag autocorrelation categories for the 15 year data series of the North River simulations (left column) and the 25 year data series simulations of the Ford Arm simulations (right column). R^2_{Adj}values from correlations in real brood tables are presented in the panel that matches the autocorrelations in the real brood table.

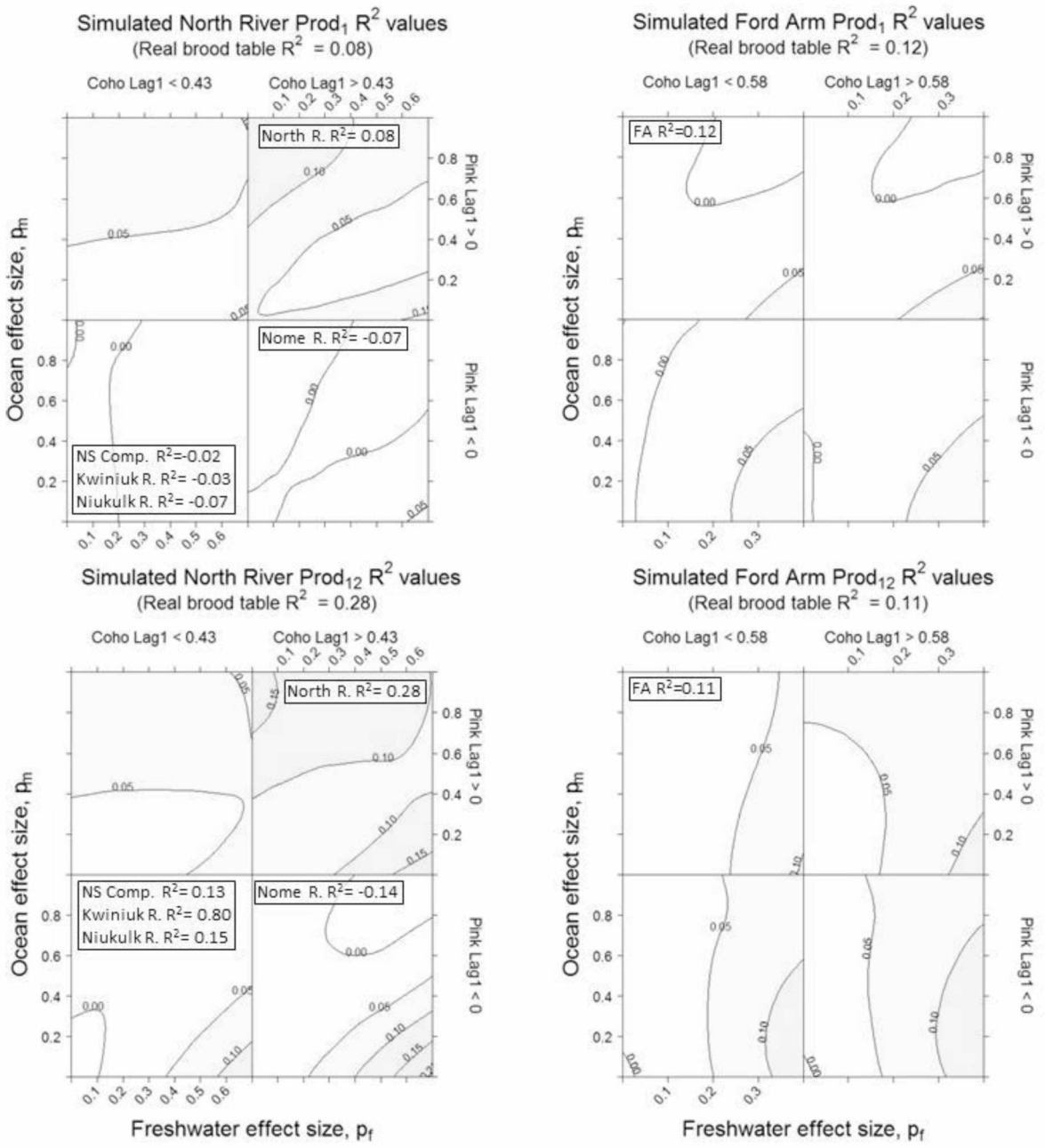

Fig 1.3. Smoothed contour plots of the average R^2_{Adj}values of $Prod_1$ (top row) and $Prod_{12}$ (bottom row) correlations as a function of freshwater (p_f) and ocean effect (p_m) sizes for each combination of Coho and Pink salmon first lag autocorrelation categories for the 15 year data series of the North River simulations (left column) and the 25 year data series simulations of the Ford Arm simulations (right column). R^2_{Adj}values from correlations in real brood tables are presented in the panel that matches the autocorrelations in the real brood table.

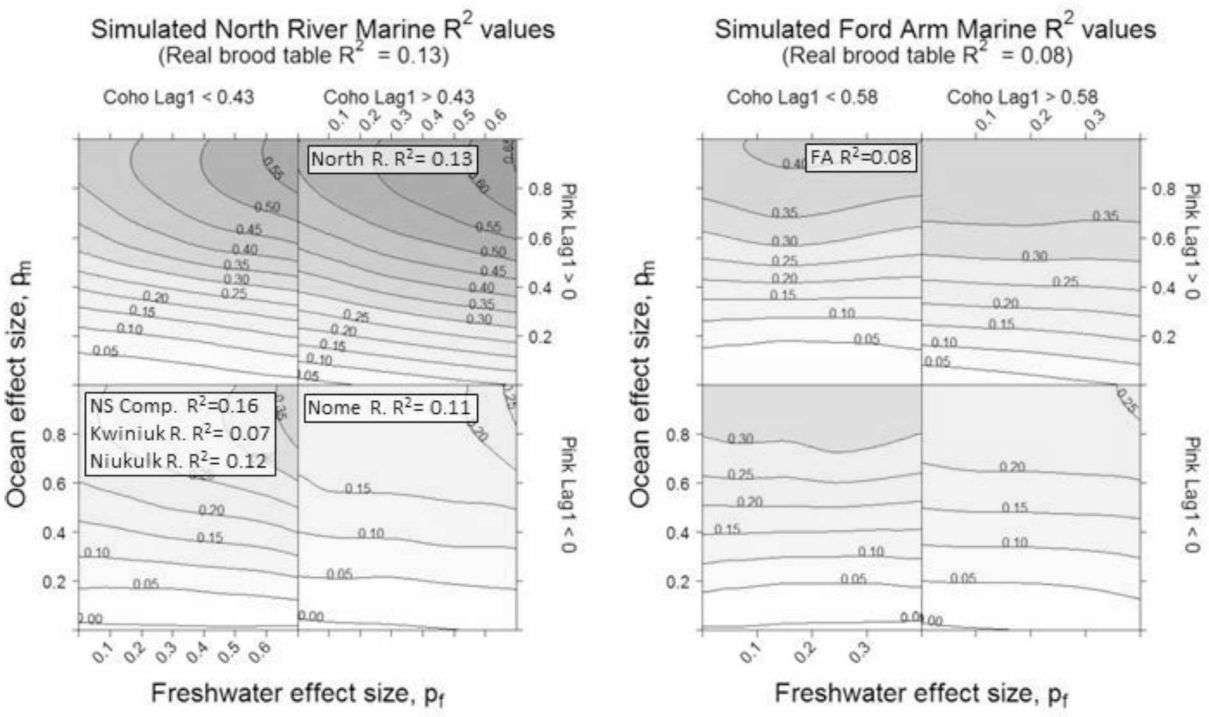

Fig 1.4. Smoothed contour plots of the average R^2_{Adj}values of *Marine* correlations as a function of freshwater (p_f) and ocean effect (p_m) sizes for each combination of Coho and Pink salmon first lag autocorrelation categories for the 15-year data series of the North River simulations (left) and the 25-year data series simulations of the Ford Arm simulations (right). R^2_{Adj}values from correlations in real brood tables are presented in the panel that matches the autocorrelations in the real brood table.

Appendices

Table 1.A.1. Brood table of Pink Salmon escapement and returns in the North River (Menard et al. 2013).

Year	Escapement	Recruits	ln(Residual) from Ricker model
1996	332,539	74,045	-1.52
1997	127,926	48,993	-1.17
1998	74,045	69,703	-0.32
1999	48,993	24,737	-0.96
2000	69,703	321,756	1.27
2001	24,737	280,212	2.13
2002	321,756	1,149,294	1.24
2003	280,212	1,670,934	1.72
2004	1,149,294	2,169,890	1.36
2005	1,670,934	583,320	0.15
2006	2,169,890	240,286	-0.54
2007	583,320	189,939	-0.91
2008	240,286	150,807	-0.57
2009	189,939	123,892	-0.58
2010	150,807	137,006	-0.28
2011	123,892	46,668	-1.19
2012	137,006	193,260	0.15
2013	46,668		
2014	193,260		

Table 1.A.2. Brood table of Coho Salmon escapement and returns in the North River (Menard et al. 2013, Soong et al. 2008).

Year	Tower Count	% Run Counted	North River Escapement	Norton Sound Subdistrict 6 Commercial Harvest	Norton Sound Subdistrict 6 Subsistence Harvest	Unalakleet River Sport Fish Harvest	Estimated North River Harvest[a]	Total North River Returns	% Age 1.1	% Age 2.1	% Age 3.1	Age 1.1 Returns	Age 2.1 Returns	Age 3.1 Returns	Brood Year Returns[b]
1996[c]	1,197	0.05	14,133[c]	52,200	15,963	3411	7,374	21,507	3.3	92.0	4.7	717	19,786	1,004	19,595
1997	5,768	0.87	6,610	26,079	9,120	2784	3,964	10,574	10.4	85.2	4.4	1,096	9,008	470	10,263
1998	3,361	0.66	5,114	24,534	11,825	2742	4,154	9,268	0.0	93.3	6.7	0	8,647	621	5,206
1999	4,792	0.99	4,861	10,264	10,250	2691	2,601	7,461	0.0	92.2	7.8	0	6,879	582	7,255
2000	6,959	0.66	10,589	29,803	9,487	4103	4,529	15,118	0.0	96.9	3.1	0	14,649	469	15,906
2001	12,383	1.00	12,383	15,102	9,520	2766	2,975	15,358	4.0	63.8	32.2	614	9,799	4,945	25,416
2002	2,966	0.98	3,022	1,079	8,301	2937	1,518	4,540	4.2	84.3	10.2	191	3,827	465	13,417
2003	5,837	1.00	5,839	13,027	6,192	1604	2,213	8,052	11.5	79.0	9.5	926	6,361	765	32,332
2004	11,187	1.00	11,188	29,282	5,978	3524	4,782	15,970	5.6	90.0	4.4	894	14,373	703	22,945
2005	19,189	1.00	19,189	63,437	6,949	3959	8,363	27,552	11.5	86.3	2.2	3,169	23,778	606	26,912
2006	9,789	1.00	9,800	98,336	7,937	4985	7,107	16,907	38.5	57.1	4.4	6,509	9,654	744	16,594
2007	19,965	0.99	20,109	88,397	6,003	4117	9,629	29,737	21.0	77.0	2.0	6,245	22,898	595	8,108
2008	15,648	1.00	15,653	77,227	5,277	6029	8,723	24,376	23.0	65.0	12.0	5,606	15,844	2,925	7,351
2009	22,266	1.00	22,291	60,230	6,966	5095	7,211	29,502	27.1	70.0	2.9	7,995	20,652	856	11,434
2010[d]	7,608	0.99	7,648	32,839	3,780	3006	3,958	11,606	23.7	70.7	5.6	2,751	8,202	654	12,086
2011[d]	3,624	1.00	3,638	29,518	2,486	2,493	3,417	7,055	23.7	70.7	5.6	1,672	4,986	397	
2012[d]	3,258	0.83	3,915	22,274	4,558	3,283	3,093	7,008	23.7	70.7	5.6	1,661	4,953	395	
2013[d]	8,834	1.00	8,834	29,390	6,117	4,068	4,061	12,895				3,056	9,112	726	
2014[d]	4,380	1.00	4,380	63,308	7,232		7,346	11,726				2,779	8,286	661	

[a]Estimated North River harvest calculated as 0.75*0.126 (Joy and Reed 2007) *total Coho Salmon harvest (commercial, subsistence and sport)

[b]Brood year returns were calculated from the age appropriate portion of the annual returns. For example, for year 2000, brood year returns for that escapement were calculated by summing the 1.1 returns in year 2003, the 2.1 returns in 2004 and the 3.1 returns in 2005.

[c]For 1996, the tower count only covered 5% of the Coho run and estimates were derived from aerial surveys on the North River and Old Woman Rivers. These aerial counts were regressed against tower counts in overlapping years in order to produce an estimated North River tower count in 1996. The results indicated a large run of Coho in 1996 which was further substantiated by a large commercial harvest.

[d] Coho Salmon age data was unavailable. Ages were assigned based on three year average of 2006 through 2008 data.

Table 1.A.3. Brood table for Ford Arm Creek Pink Salmon escapement, harvest and recruitment.

Year	Escapement[a]	Khaz Bay Purse Seine Harvest[a]	Ford Arm Harvest[b]	Brood Year Recruits	ln(Residual) from Ricker Model
1982	11,250	110,094	33,028	85,453	1.04
1983	42,500	155,351	46,605	198,281	0.62
1984	47,500	126,510	37,953	55,397	-0.76
1985	67,750	435,104	130,531	151,819	-0.07
1986	38,825	55,239	16,572	57,230	-0.54
1987	146,750	16,897	5,069	178,668	-0.52
1988	56,855	1,250	375	106,573	-0.27
1989	140,750	126,394	37,918	261,480	-0.11
1990	103,115	11,528	3,458	260,742	0.13
1991	216,750	149,099	44,730	76,650	-1.61
1992	199,933	202,696	60,809	330,368	-0.10
1993	76,000	2,168	650	408,397	0.83
1994	184,738	485,433	145,630	469,098	0.30
1995	225,000	611,324	183,397	104,817	-1.32
1996	396,113	243,283	72,985	143,010	-1.23
1997	82,355	74,874	22,462	1,346,874	1.95
1998	95,433	158,591	47,577	590,111	1.00
1999	1,275,000	239,579	71,874	520,727	0.67
2000	377,500	708,702	212,611	392,976	-0.21
2001	450,000	235,758	70,727	565,313	0.13
2002	242,500	501,588	150,476	393,396	-0.04
2003	437,500	426,043	127,813	632,873	0.24
2004	207,500	619,654	185,896	485,636	0.26
2005	400,000	776,243	232,873	485,050	-0.01
2006	201,250	947,953	284,386	283,028	-0.26
2007	232,500	841,832	252,550	353,722	-0.12
2008	207,500	251,760	75,528		
2009	282,750	236,572	70,972		

[a]Shaul et al. 2014

[b]Modeled as 0.3 * Khaz Bay purse seine harvest

Appendix 1.B: Derivation of Simulation Models. To describe the population dynamics of Coho Salmon, an age stratified multistate model (Moussalli and Hilborn 1986) was utilized such that returns for brood year *t* were modeled as

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1 + \left(\frac{\alpha_1}{\beta_1} + \frac{\alpha_1 \alpha_2}{\beta_2}\right) S_t} e^{\in_{t+a}} \quad (1)$$

where C_a was the proportion of Coho Salmon from brood year *t* returning at age *a*, α_1 was the per capita increase in the population at low densities in freshwater, α_2 was the per capita survival in the population at low densities in the ocean, β_1 represented the freshwater productive capacity, β_2 represented the marine productive capacity and S_t was the number of adult spawners in year *t*. $\in_{t+a}$ was the error term describing deviation from expected returns and was subscripted to time *t+a* such that it referenced the year that Coho Salmon would return to spawn relative to brood year *t*.

To describe Pink Salmon population dynamics a Ricker spawner recruit model (Ricker 1975) was utilized such that returns from brood year *t* were described as

$$R_t^P = \alpha^P S_t^P e^{(-\beta^P S_t^P)} + \in_t^P \quad (2)$$

where α^P determined population growth at low densities, β^P represented carrying capacity for the system and $\in_t^P$ represented the error term describing deviation from expected returns (the superscript ^{P} was utilized to differentiate Pink Salmon model parameters from Coho Salmon model parameters).

Freshwater Effects: Coho Salmon life history consists of freshwater residency which ranges from one to three years and an ocean stage of one year resulting in a total life cycle that ranges from three to five years. Jacks (age-.0) were ignored in this analysis because they are not properly enumerated in escapements and they comprise only ~6% of Ford Arm Creek escapements (Shaul et al. 2014) and less than 5% of North River escapements (Joy and Reed 2007). With regards to brood years, Coho Salmon spawned in brood year *t* would rear in freshwater between years *t+1* and *t+3* depending on whether they spent one, two or three years in freshwater before smolting. Thus, three year old Coho Salmon spawners

would have spawned in year *t*, reared in year *t+1*, smolted in year *t+2* and returned to spawn in year *t+3*. A four year old Coho Salmon spawner would have reared in year *t+1* and *t*+2, smolted in year *t+3* and returned to spawn in year *t+4*.

Using this framework one would expect Coho Salmon from brood year *t* to benefit from Pink Salmon escapements in years *t+1*, *t+2* and *t+3* depending on the age at which juveniles smolt. Ignoring three year old Coho Salmon smolt (they represent only a small portion of the population (Appendix A.2 and Shaul et al. 2014)), the benefit to rearing Coho Salmon from brood year *t*, F_t, was modeled with reference to Pink Salmon escapements, S^P, as

$$F_t = f\, S^P_{t+1} \Big/ \overline{S^P} + (1-f)\, S^P_{t+2} \Big/ \overline{S^P} \tag{3}$$

where *f* was a number between 0 and 1 that described the relative importance of marine nutrients to 0-check (young-of-the-year) Coho Salmon rearing in their first summer and *1-f* represented the relative importance of Pink Salmon subsidies to 1-check juveniles in their second summer in freshwater. The value of *f* could be varied to reflect the age structure of the Coho Salmon population in question such that *f* would be larger with populations dominated by age-1 smolt and smaller with populations dominated by age-2 smolt. The number of spawning Pink Salmon in year *t+1* and *t+2* was divided by average Pink Salmon escapements, $\overline{S^P}$, to make the number relative. For modeling purposes the term F_t was standardized to γ such that

$$\gamma_t = F_t - \bar{F} \Big/ \left(\sqrt{\frac{\sum (F_t - \bar{F})^2}{n-1}} \right) \tag{4}$$

Given that Coho Salmon freshwater productivity may be limited by freshwater conditions (Bradford et al. 1997, 2000), one would expect benefits from Pink Salmon escapements to impact the overall freshwater capacity such that the β_1 term in the multistate model (1) would be affected. Thus equation (1) was modified with γ such that Coho Salmon returns from brood year *t* were described as

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1 + \left(\frac{\alpha_1}{\beta_1 + p_f \gamma_t \beta_1} + \frac{\alpha_1 \alpha_2}{\beta_2}\right) S_t} e^{\epsilon_{t+a}} \quad (5)$$

where the term p_f was a value between 0 and 1 that determined the degree to which β_1 was impacted by γ such that a value of 0 would describe a system where Pink Salmon escapements had no impact on rearing Coho Salmon (and hence equation (5) would be reduced to equation (1)). Increasing values of p_f caused β_1 to be increasingly dependent on γ.

Ocean Effects: Although the freshwater portion of Pink and Coho salmon life cycles are markedly different (Pink Salmon migrate straight to the ocean the year after spawning) the ocean portion of the life cycles are nearly identical with both species spending one year at sea before returning to spawn. Thus Coho and Pink salmon returning to spawn in a given year would have smolted in the same year and occupied the marine environment for the same period. If the two species demonstrated a similar response to ocean conditions whereby a good year for Pink Salmon was also a good year for Coho Salmon, one would expect the residuals from the spawner recruit models to be similar. This effect was modeled such that the Pink Salmon error term from equation (2), ϵ_t^P, was standardized such that

$$\omega_t = \frac{\epsilon_{t-2}^P - \overline{\epsilon^P}}{\sqrt{\frac{\sum\left(\epsilon_{t-2}^P - \overline{\epsilon^P}\right)^2}{n-1}}} \quad (6)$$

The ω_t term referenced ocean conditions in year *t*. Because equation (2) referred to returns from brood year *t*, the actual ocean year that reflects the conditions affecting those returns would be year *t+2*. Hence, for ω_t to reference the error associated with year *t*, ω_t needed to reference Pink Salmon returns from brood year *t-2*.

The Coho Salmon error term in (1) was linked to the standardized Pink Salmon residual, $\square_t$, such that

$$\epsilon_t = p_m \omega_t + (1 - p_m)\, \epsilon_t^C \quad (7)$$

where p_m was a value between 0 and 1 that determined the proportion of the error term associated with ω_t and $\in_t^C$ represented error independent of ω_t and unique to Coho Salmon. With a p_m value of 1 the error term was completely correlated with Pink Salmon residuals whereas a value of 0 allowed the error to be fully independent of ω_t.

Substituting equation 7 into equation 5 thus described Coho Salmon returns as

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1 + \left(\frac{\alpha_1}{\beta_1 + p_f \gamma_t \beta_1} + \frac{\alpha_1 \alpha_2}{\beta_2}\right) S_t} e^{[p_m \omega_{t+a} + (1-p_m) \in_{t+a}^C]} \quad (8)$$

where the error terms referenced year $t+a$, the year when each age class of the cohort would be returning to spawn. Thus the error terms from the Coho and Pink salmon models were aligned such that the error terms referenced the year when both species shared the ocean environment.

Autocorrelation: The original error term in (1) was modified to a first order autoregressive model (Quinn and Deriso 1999; Pyper and Peterman 1998) such that

$$\in_t = (1 - \phi) A_t + \phi \in_{t-1} \quad (9)$$

where ϕ was a value between 0 and 1 that determined the amount of error in year t determined by the error in the prior year, t-1, and A_t represented error independent of the prior year. Substituting (7) for A_t resulted in an error term of

$$\in_t = (1 - \phi)(p_m \omega_t + (1 - p_m) \in_t^C) + \phi \in_{t-1} \quad (10)$$

which was substituted into (8) to arrive at a complete model of

$$R_t = \sum_{a=3}^{5} C_a \frac{\alpha_1 \alpha_2 S_t}{1 + \left(\frac{\alpha_1}{\beta_1 + p_f \gamma_t \beta_1} + \frac{\alpha_1 \alpha_2}{\beta_2}\right) S_t} e^{[(1-\phi)(p_m \omega_{t+a} + (1-p_m) \in_t^C) + \phi \in_{t+a-1}]} \quad (11)$$

that incorporated the freshwater effect, the ocean effect and autocorrelation with terms p_f, p_m and ϕ determining the magnitude of each effect. This model was used to simulate Coho Salmon population dynamics under varying levels of p_f, p_m and ϕ (Table 2).

Table 1.C.1. Data series length, first and second lag autocorrelation values, correlation coefficients (R^2_{Adj}) and p-values for correlations measured in North River, Ford Arm Creek, Norton Sound Composite, Kwiniuk River, Niukluk River, and Nome River data series.

Stock	Date Series Length	Harvest Prop.	Pink 1st Lag	Coho 1st Lag	Pink 2nd Lag	Coho 2nd Lag	Correlation (Table 1)	R^2_{Adj}	p-value
North River	15	NA	0.67	0.37	0.27	0.27	*Return*$_1$	**0.503**	**0.002**
							Return$_{12}$	**0.539**	**0.026**
							Prod$_1$	0.078	0.365
							Prod$_{12}$	**0.275**	**0.057**
							Marine	0.128	0.144
Ford Arm Creek	24	NA	0.29	0.50	0.17	0.04	*Return*$_1$	**0.112**	**0.083**
							Return$_{12}$	0.124	0.249
							Prod$_1$	<0.001	1.00
							Prod$_{12}$	0.045	0.614
							Marine	0.051	0.297
Ford Arm Creek (outlier removed)							*Return*$_1$	**0.510**	**<0.001**
							Return$_{12}$	**0.539**	**<0.001**
							Prod$_1$	**0.119**	**0.078**
							Prod$_{12}$	0.111	0.326
							Marine	0.081	0.155
Norton Sound Composite	13	NA	-0.24	0.77	0.58	0.36	*Return*$_1$	0.098	0.157
							Return$_{12}$	**0.761**	**<0.0001**
							Prod$_1$	-0.019	0.396
							Prod$_{12}$	0.127	0.204
							Marine	**0.156**	**0.066**
Kwiniuk River[a]	8	0.4	-0.45	0.38	0.39	0.02	*Return*$_1$	-0.161	0.874
							Return$_{12}$	0.407	0.117
		0.6	-0.46	0.31	0.39	-0.05	*Prod*$_1$	-0.026	0.399
		0.8	-0.46	0.25	0.39	-0.12	*Prod*$_{12}$	**0.798**	**0.008**
							Marine	0.066	0.213
Niukluk River[a]	14	0.3	-0.61	0.15	0.60	0.23	*Return*$_1$	-0.003	0.348
							Return$_{12}$	**0.498**	**0.009**
		0.5	-0.61	0.18	0.60	0.24	*Prod*$_1$	-0.074	0.747
		0.7	-0.61	0.21	0.59	0.25	*Prod*$_{12}$	0.150	0.163
							Marine	**0.124**	**0.083**
Nome River[a]	16	0.1	-0.17	0.51	0.30	0.23	*Return*$_1$	-0.071	0.954
							Return$_{12}$	**0.303**	**0.038**
		0.25	-0.17	0.52	0.30	0.26	*Prod*$_1$	-0.067	0.809
		0.4	-0.17	0.52	0.31	0.29	*Prod*$_{12}$	-0.140	0.924
							Marine	**0.114**	**0.080**

[a] For the Kwiniuk, Niukluk and Nome River data series autocorrelation values are presented for each of the three run reconstructions that varied the proportion of the sub-district harvest (Harvest Prop.) bound for the tributary in question. Correlations produced in the different harvest scenarios were similar but not presented.

Chapter 2: Bridging the gap between salmon spawner abundance and marine nutrient assimilation by juvenile salmon: seasonal cycles and landscape effects at the watershed scale

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Bridging the gap between salmon spawner abundance and marine nutrient assimilation by juvenile salmon: seasonal cycles and landscape effects at the watershed scale

Short Title: Spawner abundance and MDN use by juvenile salmon

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MANUSCRIPT HIGHLIGHTS

- Prior to salmon spawning, MDN from prior years was retained in complex habitats.
- After adult spawning, MDN use by juvenile salmon was a product of spawner abundance.
- MDN use by juveniles was related to pink and Chinook, but not chum, salmon biomass.

ABSTRACT

Anadromous Pacific salmon are semelparous and resource subsidies from spawning adults (marine-derived nutrients, or MDN) benefit juvenile salmonids rearing in freshwater. However, it remains unclear how MDN assimilation relates to spawner abundance within a watershed. To address this we examined seasonal, watershed-scale patterns of MDN assimilation in rearing coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon and compared it to spawner biomass and landscape features in a western Alaska watershed with contrasting structural complexity in two sub-drainages. Adult salmon biomass density was estimated from escapement and spawner distribution data, and MDN assimilation in juvenile salmon was estimated via stable isotopes. In the North River, MDN assimilation was lowest in early summer, prior to annual spawning migrations, increased after spawning, and peaked in late winter. In the more complex mainstem Unalakleet River, MDN assimilation was higher but varied minimally from summer through fall before increasing in late fall and winter. Summer MDN assimilation, prior to salmon spawning, was primarily a function of habitat complexity, where MDN was highest in sloughs and the more complex mainstem river. After salmon spawned, fall MDN assimilation was a function of adult pink and Chinook salmon biomass as well as MDN assimilation that occurred prior to spawning (i.e., summer MDN), but unrelated to total summer biomass (all salmon species biomass combined). Thus, MDN assimilation by juvenile salmon in the fall was a function of species-specific adult spawner abundance but seasonal patterns of MDN assimilation were masked in complex habitat where summer MDN assimilation remained high.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are semelparous anadromous fish that spawn and rear in freshwater before migrating to sea as juveniles. Pacific salmon accumulate over 99% of their adult mass while at sea and return significant amounts of marine carbon, nitrogen, and other nutrients (marine-derived nutrients; MDN) when returning to spawn and die in fresh water. Marine subsidies from spawning salmon are assimilated into freshwater and terrestrial food webs and can have large effects on multiple trophic levels. For example, MDN from carcasses and fish excretion can stimulate stream biofilms and increase microbial productivity (Bilby and others 1996; Wipfli and others 1998; Gende and others 2002; Mitchell and Lamberti 2005). Riparian vegetation, soil, and insect communities become enriched in MDN (Ben-David and Schell 1998; Reimchen and others 2002; Hocking and Reimchen 2009), and terrestrial scavengers, including birds, bears, and wolves feed on salmon and further disperse nutrients in the riparian zone (Hilderbrand and others 1999; Adams and others 2010). Within aquatic food webs, freshwater consumers, including juvenile salmon and other fishes, benefit from MDN through a variety of trophic pathways.

Pulsed marine subsidies are incorporated into juvenile salmon diets through both direct and indirect routes and can increase the quantity and quality of dietary resources by increasing ration size and energy density. Juvenile salmon feed directly on eggs and carcasses during the spawning season (Bilby and others 1998; Pearsons and Fritts 1999; Armstrong and others 2010) and on fry and smolt in the spring (Parker 1971; Hargreaves and LeBrasseur 1985; Ruggerone and Rogers 1992; Denton and others 2009). Indirectly, nitrogen and phosphorous from decaying carcasses are incorporated into aquatic and riparian food webs, thus increasing primary production and bolstering invertebrate communities (Wipfli and others 1999, 2003; Chaloner and others 2004; Hicks and others 2005; Lang and others 2006). Moreover, invertebrates colonize and feed on salmon carcasses thus increasing the size and abundance of potential food items such as midge larvae (family Chironomidae; Chaloner and others 2004; Hicks and others 2005), caddisflies (order Trichoptera; Winder and others 2005; Hicks and others 2005), stoneflies (order

Plecoptera; Ellis 1970; Wipfli and others 1998), and blowflies (family Calliphoridae; Armstrong and others 2010).

Access to marine subsidies has been shown to increase growth rates and improve overall condition in individual juvenile salmon in localized settings. Studies throughout the Pacific Northwest and Alaska have highlighted the benefit of densely spawning species such as pink (*O. gorbuscha*), chum (*O. keta*), and Sockeye (*O. nerka*) salmon to other salmonid species that rear in freshwater (Bilby and others 2003; Wipfli and others 2010; Rinella and others 2012). Juvenile coho salmon exhibited increased growth (Wipfli and others 2003; 2010) and lipid content (Heintz and others 2004, 2010) in response to pink salmon carcasses, and coho salmon and Dolly Varden (*Salvelinus malma*) also demonstrated elevated growth rates and energy content with increasing salmon spawning density in Southcentral Alaska streams (Rinella and others 2012). In British Columbia, juvenile coho salmon abundance was positively related to adult pink salmon abundance (Nelson and Reynolds 2014) and Sockeye Salmon in southwest Alaska have been shown to benefit stream dwelling salmonids, including coho salmon, Dolly Varden, and Rainbow Trout (*O. mykiss*), by increasing ration size, body condition, and growth (Scheurell and others 2007; Denton and others 2009; Armstrong and others 2010).

Watershed-scale estimates of spawner abundance (escapements) are an ostensible metric of MDN imported into watersheds, but the relationship between escapements and MDN assimilation by juvenile salmon populations remains unclear (Piccolo and others 2009; Bernard and Clark 2009). Despite a large body of literature examining MDN use by juvenile salmonids, much of the research has been limited in duration and has not focused on identifying quantitative relationships between spawner abundance and the response of juvenile salmon populations (Piccolo and others 2009). For instance, despite the pulsed timing of spawning, MDN assimilation in some fish populations lacks a seasonal pattern (Rinella and others 2013) while demonstrating seasonality in others (Reichert and others 2008; Honea and Gara 2009; Arostegui and Quinn 2018). Furthermore, much of the population-scale research to date has occurred on lake rearing Sockeye Salmon with sometimes inconclusive results (Schindler and others 2005; Uchiyama

and others 2008; Adkison 2010) while studies on stream rearing salmonids, such as coho and Chinook (*O. tshawytscha*) salmon, have been limited to correlative studies that did not investigate the MDN dynamics within the system. In one such study, pink salmon escapements during coho salmon freshwater residency were a better predictor of coho salmon recruitment than were coho salmon spawner abundance in a small (25 km^2) watershed in Southeast Alaska (Shaul and others 2014). Similarly, in the Skagit River, Washington state, coho salmon productivity was correlated with pink salmon spawning biomass in the year coho salmon reared in freshwater (Michael 1995) and coho salmon smolt abundance was correlated with pink salmon escapements in the year prior to smolting (Zimmerman 2011). While these studies match expectations from smaller scale research, the inclusion of MDN-related data would enhance our understanding of these relationships by providing a more intrinsic basis for productivity-abundance relationships.

To ultimately determine how juvenile salmon populations respond to the abundance of spawning salmon via MDN processes will require addressing several gaps in our understanding. First, a better understanding of how MDN assimilation by rearing juveniles relates to the biological characteristics of escapements, including species composition and abundance of spawners, timing of spawning events, and location and habitat of both spawners and rearing juveniles is required (Piccolo and others 2009). Second, we need to understand how MDN assimilation by juvenile salmonid populations results in nutritional benefits that can affect survival rates, including increased growth, size, and body condition. Finally, we need to understand how those nutritional benefits affect the abundance of rearing juveniles and outmigrating smolts and subsequent recruitment to the adult life stage. Developing quantitative predictions will ultimately require additional case-specific studies of these processes (Piccolo and others 2009).

The goal of this work was to address the first knowledge gap by characterizing the relationship between drainage-wide spawner abundance and MDN assimilation in juvenile salmon to better understand how spawner species, spawner abundance, and landscape features relate to MDN assimilation. As species that

rear in freshwater for one or more years Chinook and coho salmon were chosen for study given their likely and documented use of MDN. Our objectives were to assess the extent of MDN assimilation in rearing juvenile coho and Chinook salmon as a function of spawner biomass (derived from escapement and spawner distribution estimates of all species) and macrohabitat features within two sub-drainages. To address these questions, a watershed in western Alaska (the Unalakleet River) with two ongoing salmon monitoring projects located on the structurally complex mainstem and a structurally simple tributary was studied for three years (2011 – 2013). MDN assimilation in juvenile coho and Chinook salmon was measured in out-migrating smolt and in rearing parr before and after the arrival of spawning adult salmon.

METHODS

Overview: We measured the stable nitrogen (N) and carbon (C) isotopic composition of juvenile salmon tissue before (summer) and after annual spawning by adult salmon (fall and late fall) because $\delta^{15}N$ and $\delta^{13}C$ values of marine organic material are typically higher than those in terrestrial and freshwater environments and thus can be used to differentiate between sources (Bilby and others 1998, Chaloner and others 2002; Wipfli and others 2003). Returning adult salmon cease feeding in freshwater, thus retaining marine signatures which can be used to trace MDN through recipient ecosystems (Kline and others 1990, 1993; Chaloner and others 2002). We approximated spawner biomass throughout the watershed from species-specific escapements measured at a weir and counting tower and spawner distribution estimates derived from radio-telemetry and carcass surveys. MDN assimilation in juvenile salmon tissue was evaluated in two sub-drainages of varying complexity, in channel, slough, and pond habitat, and as a function of spawner biomass and macrohabitat features such as river size, sinuosity, and distance from the ocean.

Study area: The Unalakleet River drains approximately 4,800 km^2 of the Nulato Hills into the eastern end of Norton Sound on the west coast of Alaska (63.878°N, 160.605°W) (Figure 1). The North River is the largest tributary and the confluence occurs 7.2 km above the Unalakleet River mouth. The North River is characterized by a narrow valley with low sinuosity and minimal off-channel habitat, while the

Unalakleet River is characterized by a broad, u-shaped valley with greater sinuosity and large amounts of off-channel habitat such as sloughs and ox-bows (Figure 1).

The watershed supports populations of Chinook, coho, chum, pink, and sockeye salmon. Escapements are monitored annually on the North River with a counting tower and on the Unalakleet River above its confluence with the North River with a weir (Menard and others 2013) (Figure 1). In terms of anadromous biomass, pink salmon are the dominant species in the system (5-year average of 67 and 54% of biomass in North and Unalakleet rivers, respectively), followed by chum (17 and 34%) and coho salmon (14 and 11%). Chinook salmon constitute 3 and 0.6% of the annual anadromous biomass imported to the North and Unalakleet river watersheds while the Sockeye Salmon biomass is trivial (Menard and others 2013). pink, chum, and Chinook salmon begin their spawning migration in late June and have finished spawning by early August. coho salmon spawn in September and October (Menard and others 2013).

Spawner biomass density estimates: To understand how watershed-scale spawner abundance relates to MDN assimilation in juvenile salmon it was necessary to translate abundance estimates to biomass estimates to account for variation in size across salmon species. To do so we estimated spawning salmon biomass per each 10-km section of river (kg/km^2) using data on spawner distribution, abundance, and species-specific weights. For pink salmon, spawning distribution was estimated from carcass counts in 2012 and 2013, when carcasses deposited on beaches on the inside of river bends were counted between 6-8 August of both years. Counts were converted to density using the length of beach surveyed. Proportional distribution of pink salmon was determined by dividing carcass densities for each 10 km river section by the sum of all 10-km carcass density estimates. Pink salmon spawning distributions were similar between 2012 and 2013 and the average of the two years was used to represent the distributions in 2010 and 2011. To determine the spawning distribution of coho, Chinook, and chum salmon, we used radiotelemetry location data from the Alaska Department of Fish and Game (ADF&G). During these studies, the spawning distribution of each species varied minimally between years (Joy and others 2005;

Estensen and others 2005; Joy and Reed 2006, 2007, 2013, 2014; Estensen and Hamazaki 2007); therefore, telemetry data from all years were pooled. For each species, the number and proportion of radio-tagged fish migrating to each 10 km river section were counted and analyzed using ArcMAP Spatial Analyst (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

Spawner abundance per species, year (2010 – 2013), and 10-km river section was determined by multiplying escapement estimates at the North River counting tower and Unalakleet River weir (Menard and others 2013) by the proportion of spawners in each 10-km river section. The resulting spawner abundances were converted to biomass using species-specific mean weights (Menard and others 2013). The volume of water passing through each 10 km section was approximated by the size of the watershed (i.e. catchment; km^2) upstream of the downriver start of the section, calculated using a digital elevation model (DEM) and ArcMAP Spatial Analyst (Figure 1). Watershed size was closely correlated with bank full stream width ($R^2 = 0.82$) but because width increases more quickly than depth as one descends a watershed (i.e., stream channels generally become relatively wider and shallower; Rosenfeld and others 2007) we believed catchment size to be the more accurate descriptor of river volume and size at study sites. Absent significant differences in precipitation throughout a relatively small drainage, the amount of water passing through any particular point in the river should largely depend on the size of the upstream watershed. Hence, spawner biomass was converted to biomass density per reach by dividing the estimated biomass in each 10-km reach by the watershed size (km^2) above that location (referred to as "biomass" from this point forward; Appendix A.2).

Juvenile salmon sampling: Juvenile coho and Chinook salmon were captured in 2011 – 2013 before and after the arrival of spawning adult salmon, and during the spring smolt migration. For smolts, stable isotope samples were obtained from fifty smolts of each species captured in the lower end of the North and Unalakleet rivers (above their confluence; Figure 1) over the course of the smolt migration (mid-May to July 1, depending on ice-out). Smolts were captured with a fyke net (1.2 m high by 1.5 m wide) in the

North River and a 2.4 m diameter rotary screw trap (EG Solutions, Corvallis, OR) in the Unalakleet River.

We sampled rearing age-0 Chinook and age-0, -1 and -2 coho salmon (hereafter referred to as parr) at sites distributed throughout the watershed (Figure 1) during early summer (June 12 – July 12), , mid-fall (August 22 – September 12), late fall (September 20 – October 5) and winter (March 4 – 14). At each site, parr were sampled in main-channel and off-channel habitats (site 11 was an exception where only channel habitat was sampled). Sampling of channel habitat occurred in woody debris along cut banks. Off-channel sampling occurred in lentic water bodies that were either an open-mouth slough (sites 3, 7 and 8) or a pond with minimal connectivity to the mainstem (sites 2, 6 and 10). Parr were sampled by soaking baited minnow traps for two hours and approximately 15 fish per species and habitat type (channel or off-channel) were sampled during each event. Winter samples were taken from a subset of locations (Sites 2, 3, 6 and 8), in March 2012 and 2013, by fishing minnow traps through holes in the ice.

Sampled parr and smolts were anaesthetized using diluted clove oil solutions (20 μL clove oil/L water) (Cho and Heath 2000), identified to species, and measured to the nearest mm (fork length). A caudal fin clip (<0.25 cm^2) was excised and frozen for stable isotope analysis (Sanderson and others 2009; Hanisch and others 2010). Chinook salmon in all years and coho salmon in 2011 were released after recovering from anesthetic. coho salmon sampled in 2012 and 2013 were sacrificed as part of a related project (Joy and others, unpublished manuscript).

Estimating MDN assimilation in juvenile salmon tissue: To determine the proportion of juvenile salmon tissue derived from MDN, we measured stable isotope ratios in caudal fin clips of parr and smolts and, using mixing models, compared those ratios to control samples representing minimal MDN and MDN sources. The stable isotope signatures of juvenile salmon were obtained from fin clips because they accurately reflect the stable isotope signature found in muscle tissue, they can be obtained with non-lethal sampling, and processing is simpler (Sanderson and others 2009; Hanisch and others 2010). Isotopic turnover time in growing juvenile fish tissue (the time lag before the stable isotope value in the tissue

reflects the change from one food source to the new source) was assumed to be three to four weeks (Sakano and others 2005) and the timing of fall sampling (four weeks after peak spawning by pink, chum and Chinook salmon) was intended to capture potential MDN assimilation.

Stable isotope signatures of MDN sources were obtained from adult salmon muscle tissue, eggs, and pink and chum salmon smolts. Salmon muscle and egg samples were obtained from fishermen in the village of Unalakleet, at the mouth of the river. pink and chum salmon smolt were taken from the North River fyke net and Unalakleet River rotary screw trap.

Stable isotope signatures of minimal MDN sources were established using trophic corrected Ninespine Stickleback (*Pungitius pungitius*) and juvenile coho salmon obtained from three locations. We used these control samples not because they were prospective diet items for rearing coho and Chinook salmon but because their isotope signatures would reflect the prey available to juvenile salmon in areas receiving minimal MDN. Thus in order to reflect isotopic signatures of the diets the stable isotope signatures of these samples were shifted downward by the trophic enrichment factors of 3.5‰ (SD = 0.18) and 1.3‰ (SD = 0.30) for $\delta^{15}N$ and $\delta^{13}C$ respectively (McCutchan and others 2003). Sampling invertebrates would have been ideal, but would have required extensive sampling that would have reduced the resources available for examining MDN assimilation across time and space. In contrast, sampling numerous individual fish from the control areas provided a broad range of stable isotope signatures that ultimately integrated available prey items in these areas and offered a more complete trophic picture. Juvenile coho salmon fin clips from the upper reaches of the North River (Figure 1) served as *channel control* samples given that the abundance of spawning Chinook and coho salmon is minimal (Joy and Reed 2007, 2014), chum salmon were never tracked to this area (Estensen and others 2005; Estensen and Hamazaki 2007) and pink salmon carcasses were never detected there. Minimal MDN *off-channel control* values were established with Ninespine Stickleback collected from off-channel sampling Sites 2 and 6 (Figure 1) in the early summer sampling period, prior to seasonal spawning events and during low water periods. Stickleback samples were used in lieu of juvenile salmon as salmon in those areas would

have migrated into those ponds from channel habitat where they emerged from gravel and were exposed to MDN from pink, chum, Chinook, and coho salmon. Sticklebacks were regarded as unlikely to occupy and feed in channel habitats given their preference for weedy backwaters (Coad and Power 1973).

Because lipids are depleted in ^{13}C relative to other tissues and can thus obscure dietary signals, it is necessary to either extract lipids from samples prior to measuring stable isotope ratios or correct for the presence of lipids post-analysis (Post and others 2007). We removed lipids prior to stable isotope analysis for all MDN source samples (adult salmon muscle, eggs and pink and chum salmon smolts), and Ninespine Stickleback samples using repeated rinses with a chloroform and methanol mixture (2:1 ratio by volume; DeNiro and Epstein 1977). We chose to remove lipids because potential dietary items likely had a broad range in lipid content, ranging from high in salmon eggs to low in some invertebrate taxa, and we further expected seasonality in the lipid content of potential dietary resources. Lastly, the $\delta^{13}C$ values of MDN differ from freshwater and terrestrial values therefore providing a strong argument for lipid normalizing diet items to evaluate MDN assimilation over time and space. For juvenile salmon fin clips, including channel control samples, we corrected for the presence of lipids post-analysis. Using a subset of coho salmon smolts (n=27), early summer parr (n=27), and fall parr (n=26), we split fin clips into paired samples and extracted lipids from one of the two pairs prior to stable isotope analysis. We then compared $\delta^{13}C$ signatures of the paired fin clip samples (lipid-extracted versus raw sample) and used the average difference for each seasonal sample to correct lipid biases in $\delta^{13}C$ signatures of the remainder of fin clip samples by season.

To prepare samples for laboratory analysis, samples were desiccated for 48 hours in a drying oven at 60°C. Dried fin clips were cut with a razor blade while whole ink and chum salmon fry and egg samples were ground to powder with mortar and pestle. Between 0.5 and 0.8 mg of material was placed into Costech 5 x 9-mm tin capsules (Valencia, California) and sent to the U.S. Geological Survey stable isotope laboratory in Denver, Colorado, where $\delta^{15}N$ and $\delta^{13}C$ values were determined by continuous flow-isotope ratio mass spectrometry. Nitrogen and carbon isotope ratios were measured using a Carlo Erba

NC1500 elemental analyzer (Thermo Scientific, Waltham, Massachusetts, USA) interfaced to an Optima mass spectrometer (Micromass, Manchester, UK) (Fry and others 1991). Results are reported utilizing δ-notation as deviations in parts per thousand (‰):

$$\delta X = \left({}^{R_{sample}}\!/_{R_{standard}} \right) - 1$$

where X is the rare isotope (^{15}N or ^{13}C) and R is the appropriate isotope ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). Isotopic data were normalized to USGS 40 (-26.24 and -4.52‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) and USGS 41 (37.76 and 47.57‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively). Analytical error, assessed through replicate measures of ~10% of analyzed samples, averaged 0.2%. In-house standards and replicate measures of samples were used as quality control checks; reproducibility was better than 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ (data not shown).

MDN assimilation describing the proportion of juvenile salmon tissue derived from MDN was estimated via the Bayesian mixing model MixSIAR (Moore and Semmens 2008; Stock and Semmens 2013). MDN assimilation was calculated by species, site, habitat, and sampling occasion. Sources for the mixing model were taken from the marine, channel control, and off-channel control samples described above, and entered as raw values (Figure 2). The mixture model used trophic enrichment values of +3.5‰ (SD = 0.18) and +1.3‰ (SD = 0.30) for $\delta^{15}N$ and $\delta^{13}C$ respectively (McCutchan and others 2003). Stable isotope values from control samples were shifted downward by the trophic enrichment factors to reflect the isotope signatures of dietary resources. Models included "individual" as a random effect and the 'very long' option was employed for Markov chain Monte Carlo (MCMC) run lengths using '' as appropriate for models including "individual" as a random effect (Stock and Semmens 2016; Stock and others 2018; supplemental 1) The Gelman-Rubin, Heidelberg-Welch and Geweke diagnostics were used to ensure convergence of the MCMCs.

Relationship between juvenile salmon MDN assimilation, spawner biomass and landscape features: To determine how MDN assimilation in juvenile salmon tissue varied relative to spawner biomass and

landscape features, we used mixed effects generalized linear models (GLMMs) (Madsen and others 2011; Stroup 2012) and multi-model inference to estimate the importance and effect of variables (Burnham and Anderson 2002). To examine seasonality and general landscape trends in MDN assimilation, we examined MDN assimilation throughout the annual cycle as a function of season (early summer, fall, late-fall, winter, spring smolts), juvenile species (Chinook and coho salmon), river (mainstem Unalakleet versus North River), habitat (slough, pond or channel), watershed area (km^2), bank full width (m), distance from the ocean (in river km), and sinuosity (channel length/downvalley length). Bank full width was calculated for each sampling site by taking the average of three measurements at each site. Sinuosity was calculated for each 10 km river section by dividing river length (10 km) by the downvalley length as estimated with ArcGIS.

To examine how MDN assimilation in early summer (prior to annual spawning migrations) and fall (after spawning migrations and including late fall sampling) varied as a function of spawner biomass, MDN assimilation was modelled as a function of the most recent spawning events in addition to the habitat variables described above. Thus, early summer MDN assimilation was examined as a function of adult spawner biomass estimates by species from the prior year and in addition to species-specific biomass estimates included a variable representing the total biomass of all spawning salmon (pink, chum, coho, and Chinook salmon combined). Fall MDN assimilation was examined as a function of spawning biomass during the early summer sampling period immediately prior to fall sampling, but within the same year, for pink, chum, and Chinook salmon biomass separately, as well as the total spawning biomass from the three species and the amount of MDN present before salmon spawned (early summer MDN assimilation).

Year and sampling site were modelled as random effects to control for pseudoreplication. Collinearity between variables was identified when Pearson's R^2 values exceeded 0.6 (Booth and others 1994; Dormann and others 2012). Collinearity was identified between bank full width and watershed area (Pearson's $R^2 = 0.82$), between pink salmon biomass and total early summer biomass (Pearson's $R^2 =$

0.91) and between prior year total biomass and prior year pink salmon biomass (Pearson's $R^2 = 0.86$). Collinear variables were included in the analysis, but were not included in the same model thus allowing AICc ranking to determine the most important variables.

For each analysis (early summer and fall), a global model and subsets of this model were examined to determine the most relevant variables. Akaike's Information Criterion adjusted for small sample size, AICc (Burnham and Anderson 2002), was used to rank and weight models using the glmulti (Calcagno and de Mazancourt 2010) and the MuMIn package (Barton 2016) in the statistical platform R (R Core Team 2013). We examined all possible combinations of factors and interactions while limiting model size to eight total parameters. Interactions were only included in a model if both main effects in the interaction were also included (Venables and Ripley 1997). Factors and interactions were examined for their effect on the response variable using importance (I), computed as the sum of the relative evidence weights of the models in which the term appeared (Calcagno and de Mazancourt 2010). A threshold importance of 80% was used to denote "significance" (Calcagno and de Mazancourt 2010; Galipaud and others 2014). Conditional (proportion of variation explained by all model effects, including random effects) and marginal (proportion described by fixed effects) R^2 scores were calculated from the best model as a gauge of model fit and explanatory power (Madsen and Thyregod 2010; Stroup 2012; Galipaud and others 2014).

To visualize results, model averaged results were used to predict the effect of spawner biomass and habitat variables on MDN assimilation while holding other variables constant. Because it is not possible to place confidence intervals on predicted values from coefficients averaged across GLMMs we predicted values for each site and year (the random effects) and used the importance value, I, to determine the significance. Plots of predicted values present multiple lines reflecting random effects of sampling site and year.

RESULTS

Overall, MDN assimilation in juvenile salmon, as predicted from model-averaged GLMMs, varied significantly among seasons, species, and rivers and as a function of habitat variables including distance from the sea, sinuosity and habitat classification (channel, slough, or pond) (Figure 3; marginal and conditional R^2 from best model = 0.52 for both). Furthermore, there were significant interactions between season and river (Table 1 and Figure 3). In the North River, MDN assimilation was lowest in early summer (prior to the arrival of spawning salmon) and increased through fall and winter. In the Unalakleet River, MDN assimilation was overall higher than in the North River (Table 1), varied minimally between early summer, fall and late fall, but was highest in winter (Figure 3 and 4). Overall, MDN assimilation was higher in coho salmon relative to Chinook salmon (Table 1). MDN assimilation was higher in sloughs and channel habitat relative to ponds, decreased with increasing river distance from the ocean, and was lower in more sinuous sections of river (Table 1, Figure 3).

In early summer, prior to the arrival of spawning salmon, variability in MDN assimilation was best explained by habitat features, with weak relationships to spawner biomass from the previous year (Table 1 and Figure 4; marginal and conditional R^2 from best model = 0.44 and 0.57 respectively). Early summer MDN assimilation was higher in the more structurally complex mainstem Unalakleet River and varied by habitat classification such that it was highest in sloughs, lowest in ponds and intermediate in channel habitat (Table 1 and Figure 5). Early summer MDN assimilation was not significantly related to any spawner biomass metrics from the previous season. There was a weak, negative relationship with coho salmon spawner biomass from the previous year in the Unalakleet River. Early summer MDN assimilation was positively related to pink salmon biomass from the previous year, although the results were not significant (Table 1). Early summer MDN assimilation was not significantly related to chum, Chinook, or total spawner biomass (all species combined) from the prior year (Table 1 and Figure 5).

After Chinook, chum, and pink salmon spawned, fall MDN assimilation was positively related to early summer MDN assimilation and pink and Chinook salmon spawning biomass from the current year, but

unrelated to chum salmon biomass (Table 1 and Figure 6; marginal and conditional R^2 from best model = 0.38 and 0.63 respectively). Biomass estimates from all species combined failed to outperform models with species-specific biomass estimates, indicating that MDN derived from different species was not additive in nature. This dynamic was also evident in a significant interaction between pink and Chinook salmon biomass (Table 1 and Figure 6). Fall MDN assimilation was not significantly related to any habitat variable (Table 1).

Ponds demonstrated a distinct pattern whereby MDN assimilation declined between seasons, except for the period between early summer and fall sampling in 2012 (Figure 4). During a high-water event in 2012, MDN assimilation in juvenile salmon in ponds matched that in adjacent channel habitat. After water levels dropped, MDN declined in ponds to values significantly below that of channel and sloughs by the following summer (Figure 4).

In the North River, out-migrating smolts (in the spring) exhibited higher MDN assimilation relative to rearing parr sampled in other seasons while Unalakleet River smolt did not (Figure 3 and Table 1). Furthermore, there was little discernable relationship to spawner biomass from the prior year in either river (Figure 7). Neither river demonstrated a straightforward relationship between prior year spawner biomass estimates and smolt MDN, although North River smolt MDN more closely mirrored pink salmon biomass than total biomass from the previous year (Figure 7).

DISCUSSION

Overview: This study demonstrated that MDN assimilation in juvenile salmon is a function of species-specific spawner abundance and seasonality in MDN assimilation may be masked by high retention of MDN in complex habitat. The MDN assimilation of juvenile salmon tissue in the structurally simpler North River demonstrated intuitive seasonal patterns, with the lowest assimilation in early summer prior to spawning and highest in over-wintering parr and out-migrating smolt (Figure 3, 4 and 8). In contrast,

the Unalakleet River demonstrated inconsistent MDN assimilation patterns over the course of the open-water season that then increased in late fall and winter (Figure 3, 4 and 8). These contrasting patterns were due to the high retention of MDN in sloughs and complex habitats coupled with declining escapements in the years preceding and during this study (Menard and others 2013; Figure 7 and 8). In the early summer and prior to annual spawning migrations, MDN retained from previous years (residual MDN) bore little relationship to the previous year's spawning biomass. Instead, MDN assimilation in juvenile salmon was more a product of habitat complexity, with MDN assimilation remaining high in complex sections of river with an abundance of well connected, open-mouthed sloughs such as the mainstem Unalakleet River (Figures 3 and 8). In the fall, after spawning by pink, chum, and Chinook salmon, MDN assimilation by juvenile salmon was a product of both residual MDN (early summer MDN assimilation) and pink and Chinook salmon spawning biomass (Figures 6 and 8), but was not significantly related to habitat variables. Thus, in the structurally simpler North River, where MDN was weakly retained between years and was evidently flushed from the system by spring snow melt, the annual increase of MDN assimilation from early summer to fall reflected annual spawning migrations even as escapements declined (Figure 3, 4 and 8). In the more complex Unalakleet River, the annual pulse of MDN delivered to the system was not evident as an increase in MDN assimilation from early summer to fall due to apparently high retention between years coupled with declining escapements (Figure 8). Indeed, in some Unalakleet River sites during some years, early summer MDN was actually higher than fall MDN (Figure 4 and 8).

MDN assimilation in juvenile salmon, spawner biomass and escapements: MDN assimilation in juvenile salmon was shown to be a function of species-specific spawning biomass estimates rather than pooled biomass estimates, suggesting that traits unique to spawner species have a profound effect on the assimilation of marine subsidies into aquatic and riparian food webs. Assimilation of MDN may be related to species-specific traits such as spawning behavior and carcass deposition, and be affected by interspecific interactions such as redd superimposition (Buxton and others 2015) and disturbance of river

substrate by salmon (i.e., bioturbation; Moore and Schindler 2008; Monaghan and Milner 2009). pink salmon were the only species whose spawner biomass was associated with both pre-spawning early summer MDN (albeit weakly) as well as fall, post-spawning, MDN assimilation. The link between pink salmon and MDN assimilation may be a function of pink salmon being both smaller bodied and more numerous than other salmon species, resulting in a more persistent and broadly assimilated, watershed level "footprint." Furthermore, juvenile coho and Chinook salmon may favor rearing habitat that overlaps with pink salmon spawning habitat, resulting from either abiotic factors (i.e., flow, gradient) as well biotic factors such as MDN use. The significance of Chinook salmon biomass on fall MDN assimilation was a surprise given that they constitute less than 1% of mainstem Unalakleet River biomass and less than 3% of North River total salmon biomass (Appendix A.1). However, the magnitude of the pink salmon biomass GLMM effect size relative to that of Chinook salmon (Table 1) may be misleading when considering the *overall* effect of each species (Figure 6). Specifically, the effect size reflects a per-kilogram influence and given that pink salmon biomass was between 37 and 168 times that of Chinook salmon biomass (Appendix A.1), the overall effect of the former is actually larger than the latter (Figure 6). Furthermore, two sampling sites were located in areas with the highest Chinook salmon spawning density (Joy and Reed 2014), which could have exaggerated their importance relative to pink salmon. Moreover, the negative interaction between pink and Chinook salmon biomass in the fall may have signified interspecific interactions (bioturbation) or indicate that MDN assimilation from the two species is an "either-or" proposition dependent on fish distribution and behavior within sampling sites.

Bioturbation effects may explain why chum salmon were not linked to MDN levels in either early summer or fall (and why combined biomass estimates did not outperform pink salmon biomass estimates) despite comprising between 14 and 65% of early summer spawning biomass (Appendix A.1). Bioturbation may also explain the counterintuitive, inverse relationship between early summer MDN and coho salmon spawner biomass from the prior fall in the Unalakleet River. Bioturbation can redistribute sediments and biologically available nutrients, and as a result, redd construction by spawning salmon can

greatly reduce the residence time of dissolved MDN (Buxton and others 2015). Ultimately, bioturbation can affect the uptake of MDN in food webs (Moore and Schindler 2008), and decrease the abundance of benthic invertebrates (Monaghan and Milner 2009). Chum salmon are larger bodied than pink salmon and their spawning behavior may have relatively large bioturbation effects, such that MDN derived from chum salmon is ultimately unrelated to their spawning distribution. Support for this idea was provided by research in British Columbia that demonstrated that while spawning pink salmon abundance explained juvenile coho salmon abundance in both early summer and fall, chum salmon spawner abundance was inversely related to juvenile coho salmon abundance (Nelson and Reynolds 2014). Chum salmon were observed displacing juvenile coho salmon and the authors suspected bioturbation effects (Nelson and Reynolds 2014). Bioturbation from fall spawning coho salmon in this study may act similarly, thus mobilizing MDN related resources in late fall (after our sampling events). By the following summer, MDN was lower in relation to coho salmon spawning biomass from the prior year, having accumulated in sloughs and complex sections of river (Figure 5).

Habitat characteristics related to MDN retention from one year to the next: River structure and complexity demonstrated a modulating effect on MDN retention, as habitat and river characteristics were the biggest determinants of marine-nutrient assimilation in juvenile salmon prior to annual spawning (Figure 4). Watersheds with faster flushing rates (the time it takes for turn-over in the waterbody) may be less likely to retain MDN (Gross and others 1998; Holtham and others 2004) and have less woody debris to catch and retain carcasses (Cederholm and Peterson 1985). Habitat complexity increases biodiversity and system stability, consequently increasing nutrient capture (i.e. MDN) in aquatic systems (Minshall and others 1992; Cardinale and others 2002). Lotic-lentic exchanges provide large fluxes of plankton and detrital matter for filter feeders such as chironomid larvae (*Rheotanytarsus* spp.) which can reach very high densities downriver of such interfaces, remove large amounts of suspended organic matter (including MDN) and assimilate those nutrients into benthic food webs (Thorpe 2002; Woodward and Hildbrew 2002). Thus after winter and spring flooding, pre-spawner MDN assimilation was highest in open-

mouthed sloughs and in complex river sections with abundant lotic-lentic exchanges. These results partially explain why pulsed MDN subsidies persist from one season to the next in some systems (Rinella and others 2013), but decline after spawning in other systems (Reichert and others 2008; Honea and Gara 2009) (Figure 8). Structurally simple rivers demonstrate seasonal cycles of MDN that mirror annual spawning migrations given less retention of MDN from year to year (Figures 3, 4 and 8). In contrast, structurally complex systems show less distinct cycles as high retention of past years' MDN interacts with MDN from the latest spawning migration (Figures 3, 4 and 8). During periods of declining spawner abundance (as occurred during this study), annual pulses of MDN may thus be masked by high retention of MDN in complex habitat (Figure 3 and 8).

Alternatively, apparent retention of MDN in off-channel habitat may be conflated with other environmental factors that affect enrichment of the rare isotope (^{15}N or ^{13}C) and thus could mistakenly be interpreted as MDN. For instance, soil development can affect ^{15}N loading and potentially present as a marine signal (D'Amore and others 2011). However our use of both N and C in the mixing models would help to differentiate our MDN end member from non-MDN. Water velocity can also affect $\delta^{13}C$ and $\delta^{15}N$ signatures such that the heavier endmembers accumulate in periphyton where stream velocity is lower (Trudeau and Rasmussan 2003) and thus could be mistaken for a marine signal. However, the lentic end-member in our mixing models came from isolated ponds with negligible flow and thus provided an informative, non-MDN lentic endmember to contrast the marine signal (Figure 2).

The rapid depletion of MDN in ponds relative to slough and channel habitat (Figure 4) suggested rapid metabolism of MDN in food webs in the absence of replenishment from flooding events. Flooding events, such that occurred in 2012, force water and material from river channels back into usually semi-isolated ponds, transforming these habitats into open mouthed sloughs. Consequently, during the fall 2012 flood, MDN levels in ponds rose to match that of the main channel. Once water levels receded, MDN levels declined rapidly in ponds while slough habitat continued to exhibit much slower changes (Figure 3 and 4). While these results may be explained by fish moving into pond refuges during high

water events, the low MDN in fish remaining in ponds after water levels subsided suggest the depletion of MDN in ponds when connectivity to channel habitat became limited. This further illustrated the importance of lentic-lotic exchanges to MDN assimilation and retention.

MDN in over-wintering juvenile salmon: Several factors may have contributed to the relatively high MDN assimilation in parr during the winter, including accumulated MDN from summer spawning species, MDN assimilated from coho salmon spawning in the late fall (September – October), low metabolic rates in near freezing water and possible late winter catabolism of tissue. In the Pacific Northwest, high MDN assimilation in the winter was thought to result from the scavenging of adult coho salmon carcasses (Reichert and others 2008), while in our study MDN levels at sampling site 10 (where only coho salmon spawned) were consistently higher than minimal-MDN control samples (Figure 4). Although spawning coho salmon likely contributed to winter MDN assimilation, the negative association with MDN in the following summer suggested that retention of fall and late fall stable isotope signatures were at least as important in determining winter MDN levels. Stable isotope signatures from late fall also may be retained through winter as over-wintering salmon experience near-freezing temperatures (0°C) with little growth or tissue turnover (Perga and Gerdeaux 2005; Rinella and others 2013). Finally, the effects of late winter catabolism, whereby protein is broken down as lipid reserves dwindle, are also not fully understood (Doucett and others 1999), but could be conflated with elevated MDN assimilation. Initial lipid catabolism would result in the consumer lipids being propagated into proteins and other structural tissues which would cause isotopic enrichment of those tissues (Pecquerie and others 2010). Under continued nutritional stress and fasting, body protein itself is catabolized to fuel metabolic functions resulting in isotopic enrichment of residual protein reserves and thus consumers display higher $\delta^{15}N$ signatures than their diet (McCutchen and others 2003). In this circumstance the "diet" is the fish's own tissue and thus catabolism may increase the fish's $\delta^{15}N$ signature (Hobson and others 1993) which would consequently increase our estimates of MDN assimilation.

MDN assimilation in smolt: Out-migrating smolts of both species demonstrated high MDN assimilation with levels similar to winter and late fall parr (Figure 3). Coming out of winter, migrating smolt would have begun their migration with relatively high MDN assimilation. Subsequently, high MDN assimilation would be maintained on their way to the ocean as smolt migrated through enriched MDN areas (i.e., Site 6; Figure 1 and 4) where they preyed on pink and chum salmon smolts and aquatic invertebrates associated with early summer MDN such as chloroperlid stoneflies (Ellis 1970; P. Joy, unpublished data).

The inconsistency between smolt MDN assimilation and escapements from the prior year suggests that pre-smolt habitat use and distribution, as well as spring flooding events, affected smolt MDN levels more so than escapements. Specifically, because early summer MDN assimilation in rearing parr was a function of occupied habitat and only weakly related to the previous years' spawner biomass, it is likely that smolts experienced similar relationships in the spring prior to emigrating. Additionally, spring floods associated with thawing ice and snow are often dynamic and dramatic events that redistribute nutrients (including MDN) and organisms (including pink and chum salmon smolt and aquatic invertebrates) within the watershed (Herbst and Cooper 2010; Cross and others 2011). Spring thaws were mild and tempered in 2011 and 2012, while break-up in 2013 was dramatic and preceded by prolonged and substantial flooding in fall 2012. Coincidently, the noticeably higher MDN assimilation in the Unalakleet River in 2013 relative to 2011 and 2012 perhaps suggests increased transport of marine nutrients and material to downriver portions of the watershed, thus enriching aquatic food webs utilized by out-migrating smolts with MDN. Inferences regarding MDN assimilation in smolt and spawner biomass from the prior year are of course limited by only three years of data and a better understanding of smolt distribution prior to emigration, as well as longer term data series, are required to understand these dynamics.

Implications of turnover time: Turnover time, or the amount of time it takes the stable isotope signature of diet items to integrate into fish tissue, could have implications for this study, particularly as it pertains

to the peak MDN assimilation and issues of fish movement. Although not examined in this study, turnover time in fish tissue was assumed to be three to four weeks given juvenile fish that are maximizing growth (Sakano and others 2005). The timing of fall sampling was thus scheduled for approximately three to four weeks after peak spawning by pink, chum, and Chinook salmon. However, late fall and winter sampling revealed that MDN levels increased steadily from fall through late winter (Figure 3), a likely reflection of MDN being incorporated into all levels of the food web upon which juvenile salmon feed. While we succeeded in capturing the pulse of marine nutrients with fall sampling, higher MDN in late fall suggests that optimal sampling for peak assimilation would be towards the end of September and early October. Winter MDN levels were even higher than late fall, although a better understanding of how late winter catabolism impacts isotope signatures is needed to understand whether peak assimilation occurs during winter months. An ideal approach to addressing peak assimilation would be a longitudinal study where fewer sites are visited more frequently over several years.

Given turnover time, significant fish movement could also obscure results if there were large migrations occurring in the weeks prior to sampling. However, because we described spawner biomass on a large scale (10 river km) we do not think that movement was a major issue in this study. Early summer sampling occurred well after spring break-up when spring freshets would have caused large scale movements and it is reasonable to presume that the majority of fish migrated less than 5 river km in the weeks prior to sampling (Anderson and others 2013; Armstrong and Schindler 2013; Weybright and Giannico 2018).

Although large scale movements appeared unlikely, there was evidence of limited movement within study sites between channel and off-channel sampling areas. Marked fish were observed moving between channel and off-channel habitat during sampling and during the 2012 flood there was significant movement of fish into sheltered off-channel areas which likely contributed to slough, pond, and channel habitat demonstrating similar MDN levels during that sampling period. The extent to which this impacted our results is difficult to assess, though we note that stable isotope signatures often differed

between habitats within study sites suggesting that more often than not there was minimal within site movement between habitats.

Conclusions: Our results demonstrated how MDN assimilation by juvenile salmon in a watershed is related to escapements of adult salmon when accounting for habitat and landscape features. MDN assimilation in juvenile salmon in the fall, after annual spawning migrations, was reflective of pink and, to a lesser extent, Chinook salmon biomass and escapements, but pre-spawning MDN levels were more a function of habitat complexity and much less a function of spawner biomass from the previous year. The persistence of MDN from one season to the next was thus associated with lentic-lotic exchanges, which helps explain why MDN persists in some systems (Rinella and others 2013) and exhibits seasonal pulses in others (Reichert and others 2008; Honea and Gara 2009).

Results from this study provide a foundation for incorporating MDN into salmon management models by demonstrating the link between pink and Chinook salmon escapements and MDN assimilation in rearing juvenile salmon. These results demonstrated a partial mechanism explaining observed relationships between coho and pink salmon populations in the North River (Joy and others, unpublished manuscript), Southeast Alaska (Shaul and others 2014) and the Pacific Northwest (Michael 1995; Zimmerman 2011) that are thought to result from an MDN benefit of pink salmon to coho salmon. In the absence of long term studies, these results provide initial estimates of how escapement estimates translate to MDN use by rearing juveniles. However, while we have documented assimilation and use of marine subsidies throughout the watershed, we have not documented how these relationships affect productivity of the stock. To ultimately be informative to fisheries management, environmental and biological variables must have a large influence on recruitment (Adkison 2009) and it remains unclear if the abundance of spawners in a watershed ultimately benefits juvenile salmon and freshwater productivity in a manner that is large and consistent enough to affect recruitment. The next step is to determine how MDN assimilation associated with salmon escapements in this study ultimately translates to growth, condition and abundance of juvenile salmon in a watershed (Joy and others, unpublished manuscript).

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LITERATURE CITED

Adams, L. G., S. D. Farley, C. A. Stricker, D. J. Demma, G. H. Roffler, D. C. Miller and R. O. Rye. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? Ecological Applications 20: 251-262.

Adkison, M. A. 2010. Models of the effects of marine-derived nutrients on salmon (*Onchorhynchus* spp.) population dynamics. Canadian Journal of Fisheries and Aquatic Science 67: 5-15.

Adkison, M. A. 2009. Drawbacks of complex models in frequentist and Bayesian approaches to natural-resource management. Ecological Applications, 19: 198-205.

Anderson, J. H., G. R. Pess, P. M. Kiffney, T. R. Bennett, P. L. Faulds, W. I. Atlas, and T. P. Quinn. 2013. Dispersal and tributary immigration by juvenile coho salmon contribute to spatial expansion during colonization. Ecology of Freshwater Fish 22: 30-42.

Armstrong, J. B. and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16: 1429-1441.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91: 1445-1454.

Arostegui, M. C., and T. P. Quinn. 2018. Trophic ecology of nonadromous rainbow trout in a post-glacial lake system: a partial convergence of adfluvial and fluvial forms. Canadian Journal of Zoology 96: 818-827.

Barton, K. 2016. Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package = MuMIn.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bernard, D. R., and R. A Clark. 2009. Importance of marine-derived nutrients in establishing escapement goals for Pacific salmon. American Fisheries Society Symposium 71: 147-164.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Science 53: 164-173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Science 55:1909-1918.

Bilby, R. E., E. W. Beach, B. R. Fransen, J. K. Walter, and P. A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of the American Fisheries Society 132: 733-745.

Booth, G. D., M. J. Niccolucci, and E. G. Schuster.1994. Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. US Dept. of Agriculture, Forest Service.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Buxton, T. H., J. M. Buffington, D. Tonina, A. K. Fremier and E. M. Yager. 2015. Modeling the influence of salmon spawning on hyporheic exchange of marine-derived nutrients in gravel stream beds. Canadian Journal of Fisheries and Aquatic Science 72: 1-13.

Calcagno, V. and C. de Mazancourt. 2010. Glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1-29.

Cardinale, B. J., M. A. Palmer and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415: 429-429.

Cederholm, C. J., and N. P. Peterson. 1985. The retention of coho salmon (Oncarhynchus kisutch) carcasses by organic debris in small streams. Canadian Journal of Fisheries and Aquatic Sciences 46:1222-1225.

Chaloner, D. T., G. A. Lamberti, R. W. Merritt, N. L. Mitchell, P. H. Ostrom and M. S. Wipfli. 2004 Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshwater Biology 49: 587-599.

Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Science 59: 1257-1265.

Coad, B. W. and G. Power. 1973. Observations on the ecology and meristic variation of the Ninespine Stickleback, *Pungitius pungitius* (L. 1758) of the Matamek River system, Quebec. The American Midland Naturalist 90: 498-503.

Cho, G. K. and D. D. Heath. 2000. Comparison of tricaine methanesulphonate (MS222) and clove oil anaesthesia effects on the physiology of juvenile Chinook salmon *Oncorhynchus tshawytscha* (Walbaum). Aquatic Research 31: 537-546.

Cross, W. F., C. V. Baxter, K. C. Donner, E. J. Rosi-Marshall, T. A. Kennedy, R. O. Hall Jr., H. A. W. Kelly and R. S. Rogers. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications, 21: 2016-2033.

D'Amore, D. V, N. S. Bonzey, J. Berkowitz, J. Ruegg, and S. Bridgham. 2011. Holocene soil-geomorphic surfaces influence the role of salmon-derived nutrients in the coastal temperate rainforest of southeast Alaska. Geomorphology 126(3–4):377–386.

DeNiro, M. J. and S. Epstein. 1977. Influence of diet on the distribution of carbon isotopes in animals. Geochemica at Cosmochimica Acta 42: 495-506.

Denton, K. P., H. B. Rich Jr., and T. P. Quinn. 2009. Diet, movement, and growth of Dolly Varden in response to Sockeye Salmon subsidies. Transactions of the American Fisheries Society 138: 1207-1219.

Dormann, C. F., J. Elith, S/ Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell and S. Lautenbach. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 35: 001-020.

Doucett, R. R., R. K. Booth, G. Power, and R. S. McKinley. 1999. Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights from stable-isotope analysis. Canadian Journal of Fisheries and Aquatic Science 56: 2172-2180.

Ellis, R. J. 1970. Alloperla stonefly nymphs: predators or scavengers on salmon eggs and alevins? Transactions of the American Fisheries Society 99: 677-683.

Estensen, J. L. and T. Hamazaki. 2007. Estimation of abundance and distribution of chum salmon (*Oncorhynchus keta*) in the Unalakleet River drainage, 2005. Alaska Department of Fish and Game, Fishery Data Series No. 07-03, Anchorage.

Estensen, J. L., G. L. Todd, and C. S. Monsivais. 2005. Estimation of abundance and distribution of chum salmon in the Unalakleet River drainage, 2004. Alaska Department of Fish and Game, Fishery Data Series No. 05-52, Anchorage.

Fry, B. 1991. Stable isotope diagrams of freshwater food webs. Ecology 72: 2293-2297.

Galipaud, M., M. A. F. Gillingham, M. David and F-X. Dechaume-Moncharmont. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods in Ecology and Evolution 5: 983-991.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. Bioscience 52: 917-928.

Gross, H. P., W. A. Wurtsbaugh, and C. Luecke. 1998. The role of anadromous sockeye salmon in the nutrient loading and productivity of Redfish Lake, Idaho. Transactions of the American Fisheries Society 127:1-18.

Hanisch, J. R., W. T. Tonn, C. A. Paszkowski and G. J. Scrimgeour. 2010. $\delta^{13}C$ and $\delta^{15}N$ signatures in muscle and fin tissues: nonlethal sampling methods for stable isotope analysis of salmonids. North American Journal of Fisheries Management 30: 1-11.

Hargreaves, N. B. and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Canadian Journal of Fisheries and Aquatic Science 42: 659-668.

Heintz, R. A., B. D. Nelson, J. Hudson, M. Larson, and L. Holland. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Transactions of the American Fisheries Society 133: 559-567.

Heintz, R. A., M. S. Wipfli, and J. P. Hudson. 2010. Identification of marine-derived lipids in juvenile coho salmon and aquatic insects through fatty acid analysis. Transactions of the American Fisheries Society 139: 840-854.

Herbst, D. B. and S. D. Cooper. 2010. Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. Journal of the North American Benthological Society 29: 1354-1366.

Hicks, B. J., M. S. Wipfli, D. W. Lang and M. E. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144: 558-569.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins and C. C. Schwartz. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121: 546-550.

Hobson, K. A., R. T. Alisauskas and R. G. Clark. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analysis of diet. The Condor 95: 388-394.

Hocking, M. D., and T. E. Reimchen. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. Oikos 118: 1307-1318.

Holtham, A. J., I. Gregory-Eaves, M. G. Pellatt, D. T. Selbie, L. Stewart, B. P. Finney, and J. P. Smol. 2004. The influence of flushing rates, terrestrial input and low salmon escapement densities on paleolimnological reconstructions of sockeye salmon (*Oncorhynchus nerka*) nutrient dynamics in Alaska and British Columbia. Journal of Paleolimnology 32:255-271

Honea, J. M and R. I. Gara. 2009. Macroinvertebrate community dynamics: strong negative response to salmon red construction and weak response to salmon-derived nutrient uptake. Journal of North American Benthological Society 28: 207-219.

Joy, P., A. L. J. Brase, and D. J. Reed. 2005. Estimation of coho salmon abundance and spawning distribution in the Unalakleet River 2004. Alaska Department of Fish and Game, Fishery Data Series No. 05-38, Anchorage.

Joy, P. and D. J. Reed. 2006. Estimation of coho salmon abundance and spawning distribution in the Unalakleet River 2005. Alaska Department of Fish and Game, Fishery Data Series No. 06-38, Anchorage.

Joy, P. and D. J. Reed. 2007. Estimation of coho salmon abundance and spawning distribution in the Unalakleet River 2004 - 2006. Alaska Department of Fish and Game, Fishery Data Series No. 07-48, Anchorage.

Joy, P. and D. J. Reed. 2013. Estimation of Chinook salmon abundance and spawning distribution in the Unalakleet River 2009. Alaska Department of Fish and Game, Fishery Data Series No. 10-XX, Anchorage.

Joy, P. and D. J. Reed. 2014. Estimation of Chinook salmon abundance and spawning distribution in the Unalakleet River 2010. Alaska Department of Fish and Game, Fishery Data Series No. 10-XX, Anchorage.

Kline, T. C. Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific Salmon: I, $\delta^{15}N$ and $\delta^{13}C$ evidence in Sashin Creek, Southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47: 136-144.

Kline, T. C. Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, P. L. Parker, and R. S. Scalan. 1993. Recycling of elements transported upstream by runs of Pacific Salmon: II, $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, Bristol Bay, Southwestern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50: 2350-2365.

Lang, D. W., G. H. Reeves, J. D. Hall, and M. S. Wipfli. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. Canadian Journal of Fisheries and Aquatic Science 63: 917-930.

Madsen, H. and P. Thyregod. 2010. Introduction to General and Generalized Linear Models. Chapman & Hall/CRC. ISBN 978-1-4200-9155-7.

McCutchan Jr., J. H., W. M. Lewis Jr., C. Kendall and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390.

Menard, J., J. Soong, S. Kent, and A. Brown. 2013. 2012 Annual management report Norton Sound – Port Clarence Area, and Arctic-Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 13-28, Anchorage.

Michael Jr., J. H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Science, 69: 228-233.

Minshall, G. W., R. C. Petersen and T. L. Bott. 1992. Stream ecosystem dynamics of the Salmon River, Idaho: an 8th-order system. Journal of the North American Benthological Society 11: 111-137.

Mitchell, N. L. and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. Limnology and Oceanography 50: 217-227.

Monaghan, K. A. and A. M. Milner. 2009. Effect of anadromous salmon red construction on macroinvertebrate communities in a recently formed stream in coastal Alaska. Journal of the North American Benthological Society 28: 153-166.

Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. Journal of Animal Ecology 77: 275-284.

Moore, J. W., and B. X. Semmens 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters, 11(5), 470-480.

Nelson, M. C. and J. D. Reynolds. 2014. Time-delayed subsidies: interspecies population effects in salmon. PLoS ONE 9(6): e98951.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28: 1503-1510.

Pearsons, T. N. and A. L. Fritts. 1999. Maximum size of chinook salmon consumed by juvenile coho salmon. North American Journal of Fisheries Management 19: 165-170.

Pecquerie, L., R. M. Nisbet, R. Fablet, A. Lorrain, and S. A. L. M. Kooijman. 2010. The impact of metabolism on stable isotope dynamics: a theoretical framework. Philosophical Transactions of the Royal Society B 365: 3455-3468.

Perga, M. E., and D. Gerdeaux. 2005. 'Are fish what they eat' all year round? Oecologia 144: 598-606.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Linking Alaskan salmon fisheries management with ecosystem-based escapement goals: a review and prospectus. Fisheries 34: 124-134.

Post, D. M., C. A. Layman, D. A. Albrey Arrington, G. Takimoto, J. Quattrochi, C. G. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analysis. Oecologia 152: 179-189.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reichert, W. L., C. M. Greene, and R. E. Bilby. 2008. Seasonal variations in stable isotope ratios of juvenile coho salmon (*Oncorhynchus kisutch*) from western Washington rivers. Canadian Journal of Fisheries and Aquatic Science 65: 681-690.

Reimchen, T. E., D. Mathewson, M. D. Hocking, J. Moran, and D. Harris. 2002. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in riparian zones in coastal British Columbia. American Fisheries Society Symposium XX: 1-12.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Science 69: 73-84.

Rinella, D. J., M. S. Wipfli, C. M. Walker, C. A. Stricker and R. A. Heintz. 2013. Seasonal persistence of marine-derived nutrients in south-central Alaskan salmon streams. Ecosphere 4: 1-18.

Rosenfeld, J. S., J. Post, G. Robins, and T. Hatfield. 2007. Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat. Canadian Journal of Fisheries and Aquatic Science 64: 755-767.

Ruggerone, G. T. and D. E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: implications for salmon management. North American Journal of Fisheries Management 12: 87-102.

Sakano, H., E. Fujiwara, S. Nohara, and H. Ueda. 2005. Estimation of nitrogen stable isotope turnover rate of *Oncorhynchus nerka*. Environmental Biology of Fishes 72: 13-18.

Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. Ashley Steel, and W. L. Reichert. 2009. Nonlethal sampling of fish caudal fins yields valuable stable isotope data for threatened and endangered fishes. Transactions of the American Fisheries Society 138: 1166-1177.

Scheurell, M. D., J. W. Moore, D. E. Schindler and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52: 1944-1956.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology, 86 (12), 3225-3231.

Shaul, L. D., K. F. Crabtree, K. C. Koolmo, K. M. Koolmo, J. V. Nichols, and H. J. Geiger. 2014. Studies of coho salmon and other *Oncorhynchus* species at Ford Arm Creek, 1982 – 2009. Alaska Department of Fish and Game, Fishery Manuscript Series No. 14-02, Anchorage.

Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmes. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PerrJ 6: e5096; DOI 10.7717/peerj.5096

Stock, B.C. and B.X. Semmens. 2013. MixSIAR GUI User Manual, version 1.0. http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR

Stock, B. C. and B. X. Semmens. 2016. Unifying error structures in commonly used biotracer mixing models. Ecology 97: 2562-2569.

Stroup, W. W. 2012. Generalized linear mixed models: modern concepts, methods and applications. Chapman & Hall/ CRC Press, Boca Raton, FL.

Thorpe, J. H. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Trudeau, V. and J. B. Rasmussen. 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. Limnology and Oceanography 48(6): 2194-2199.

Uchiyama, T., B. P. Finney, and M. D. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Onchorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Science 65: 1635-1648.

Venables, W. N. and B. D. Ripley. 1997. *Modern Applied Statistics with S-PLUS.* 3rd Edition. Springer-Verlag, New York.

Weybright, A. D., G. R. Giannico. 2018. Juvenile coho salmon movement, growth and survival in a coastal basin of southern Oregon. Ecology of Freshwater Fish 27: 170-183.

Winder, M., D. E. Schindler, J. W. Moore, S. P. Johnson, and W. J. Palen. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Canadian Journal of Fisheries and Aquatic Science 62: 2285-2293.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Science 55: 1503-1511.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132: 371-381.

Wipfli, M. S., J. Hudson, D. T. Chaloner and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Science 56: 1600-1611.

Wipfli, M. S., J. P. Hudson, J. P. Caouette and N. L. Mitchell. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic lveles in streamside experimental channels. Transactions of the American Fisheries Society 139: 824-839.

Woodward, G. and A. G. Hildrew. 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

Zimmerman, M. 2011. 2011 wild coho forecasts for Puget Sound, Washington Coast, and Lower Columbia. Washington Department of Fish and Wildlife, Olympia, Washington.

TABLE LEGENDS

Table 2.1. Importance and model-averaged effect sizes (and unconditional variance) from model averaged mixed effects generalized linear models of marine-derived nutrient (MDN) assimilation in juvenile coho and Chinook salmon tissue from all seasons (N=142), early summer (N=32) and fall (N=46) as a function of season (all seasons only) spawner biomass (summer and fall analysis only) and habitat variables. Habitat variables are only listed if their importance exceeded 80%. Interactions between variables are indicated with an asterisk (*).

TABLES

Table 2.1. Importance and model-averaged effect sizes from model averaged GLMMs.

Data Set	Variable	Interaction	Estimate	Adjusted Standard Error	Importance
All Seasons	Species (Chinook)		-0.063	0.023	100%
	Season (Summer)		-0.12	0.074	100%
	Season (Fall)		-0.023	0.068	
	Season (Late Fall)		0.0064	0.075	
	Season (Winter)		0.036	0.070	
	River (Unalakleet)		0.10	0.35	100%
	Sinuosity		-0.19	0.078	94%
	River km from ocean		-0.0026	0.0028	94%
	River (Unalakleet)*	Early summer	0.15	0.060	94%
		Fall	0.029	0.060	
		Late fall	0.025	0.071	
		Winter	0.064	0.069	
	Habitat (Pond)		-0.054	0.30	89%
	Habitat (Slough)		0.024	0.11	
Early Summer	River (Unalakleet)		0.25	0.83	100%
	Habitat (Pond)		0.011	0.34	93%
	Habitat (Slough)		0.037	0.096	
	Prior fall coho biomass		0.0071	0.030	57%
	Prior summer pink biomass		0.0034	0.0071	42%
	Prior summer Total biomass		0.0025	0.0048	28%
	Prior summer chum biomass		-0.0057	0.0079	14%
	Prior fall coho biomass *	Hab. (Pond)	0.027	0.0093	13%
		Hab.(Slough)	0.00013	0.0055	
		River (Unk)	-0.043	0.035	10%
		Prior sum. pink biomass	-0.00040	0.00020	7%
	Prior summer Chinook biomass		0.021	0.11	5%
	Prior year total biomass		0.0076	0.024	2%
Fall & Late Fall	Summer MDN		0.53	0.32	100%
	Pink biomass		0.0077	0.0051	90%
	Species (Chinook)		0.052	0.047	87%
	Species (Chinook) *	Summer MDN	-0.71	0.24	81%
	Chinook biomass		0.059	0.087	80%
	Pink biomass *	Chinook biomass	-0.0047	0.0020	72%
	Total summer biomass		0.0017	0.0025	9%
	Chum biomass		-0.0010	0.0044	1%

FIGURE LEGENDS

Figure 2.1. Digital elevation model of the Unalakleet River drainage, the location of the Unalakleet River weir and North River counting tower used for monitoring salmon escapements in the watershed, and the location of sampling sites (hexagons, numbered for reference) in the Unalakleet River drainage. Locations where stable isotope minimal marine-derived nutrient source (control) samples were collected are shown by triangles and include channel control samples (C) and off-channel control samples (L). Out-migrating smolts were sampled near the counting tower and below the Unalakleet River weir.

Figure 2.2. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$ values) of channel control, off-channel control, marine samples (Chinook, coho, chum and pink salmon adult muscle tissue, eggs and fry) and juvenile coho and Chinook salmon fin clip samples. The dotted line illustrates the isotopic space contained between the source data.

Figure 2.3. Predicted marine-derived nutrient assimilation in juvenile coho and Chinook salmon as a function of river, season (top row), habitat (middle row), sinuosity and distance from the ocean (bottom row) as predicted from model averaged mixed effect generalized linear models. Error bars in bar plots represent standard errors of predicted values derived from the random effects of sampling site and year. Different lines in the lower plots represent the random effects of sampling site and year, and line type represents different habitats (channel = straight lines, sloughs = short dashed lines and ponds = long dashed lines).

Figure 2.4. Marine-derived nutrient assimilation of juvenile coho salmon at three sampling sites in 2011 – 2013 as estimated from the Bayesian mixing model MixSIAR. Black circles indicate channel habitat and gray circles indicate either slough (Site 3) or pond habitats (Sites 6 and 10). Error bars represent 90% credibility intervals.

Figure 2.5. Summer (pre-spawning) marine-derived nutrient assimilation in juvenile coho and Chinook salmon as a function of river, habitat (top row) and spawning biomass of coho, pink (middle row), chum and Chinook salmon (bottom row) from the previous year as predicted by model averaged mixed effect

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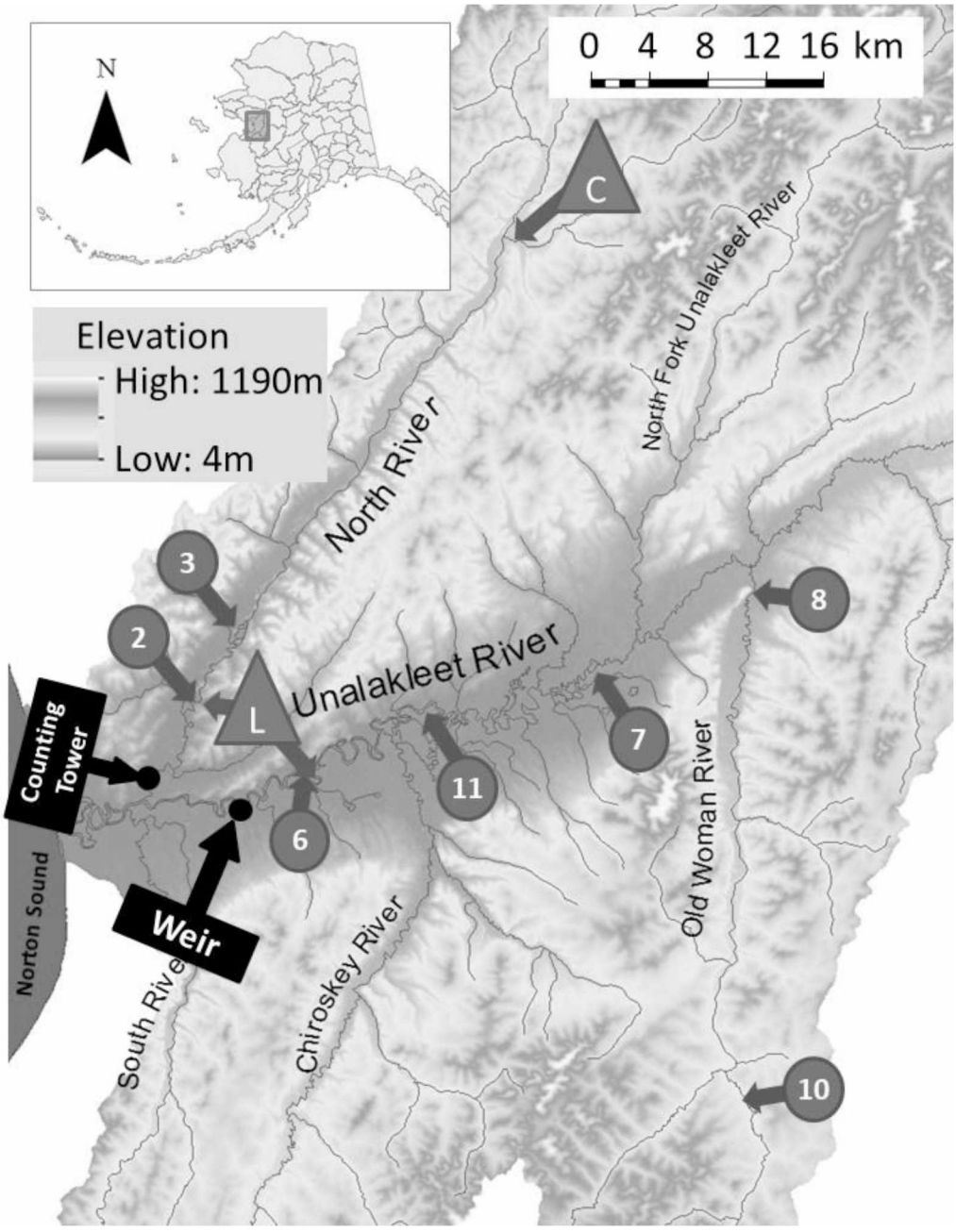
Figure 2.6. Fall (post-spawning) marine-derived nutrient (MDN) assimilation in juvenile coho and Chinook salmon as a function of spawner biomass density (left four plots and contour plot) and summer MDN assimilation (lower right plot) as predicted by model averaged mixed effect generalized linear models. Different lines in the plots represent the random effects of sampling site and year. The contour plot shows predicted fall MDN assimilation (contours) as a function of pink and Chinook salmon biomass.

Figure 2.7. Top Row: The relationship between coho salmon smolt marine-derived nutrient (MDN) assimilation for North and Unalakleet river smolt in comparison to total spawner biomass (open points and dashed line) and pink salmon biomass (filled points and solid line) estimates from the year prior to smolting. Bottom Row: Plots depicting prior year spawning biomass in bars and smolt MDN assimilation in points and lines, illustrating the declining spawner biomass that occurred during study years. Error bars represent 95% credibility intervals.

Figure 2.8. Conceptual model of how marine-derived nutrient (MDN) assimilation (proportion of tissue derived from MDN) in rearing juvenile coho and Chinook salmon relates to pink, Chinook and coho salmon spawner biomass in a highly complex (dashed line) and structurally simple (solid line) watershed. Thus, spawning pink and Chinook salmon increase MDN assimilation in juveniles, relative to pre-spawning, summer MDN levels (Figure 4) while fall spawning coho salmon decrease MDN assimilation in rearing juveniles in the following summer. MDN in rearing juveniles is retained between seasons in more complex sections of river and thus the amplitude of seasonal MDN fluxes is less, particularly during a period of declining escapements as conceptualized here.

FIGURES



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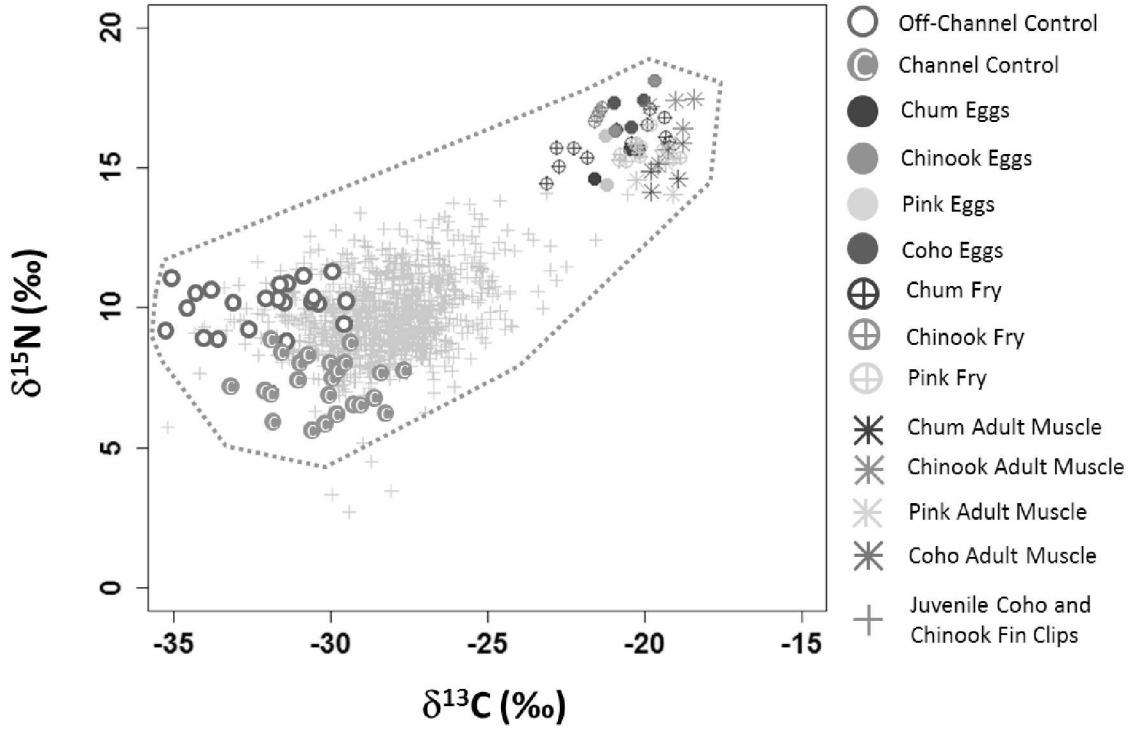

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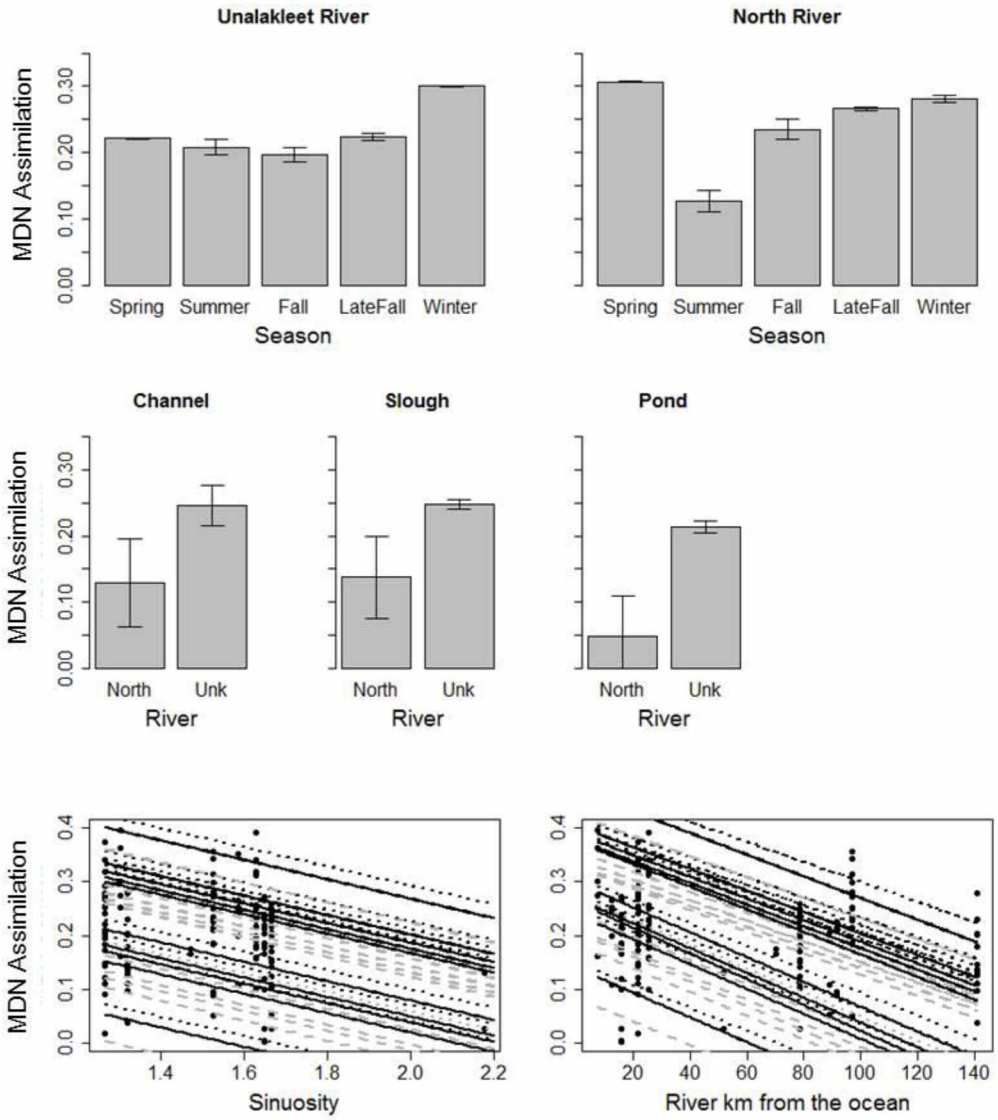

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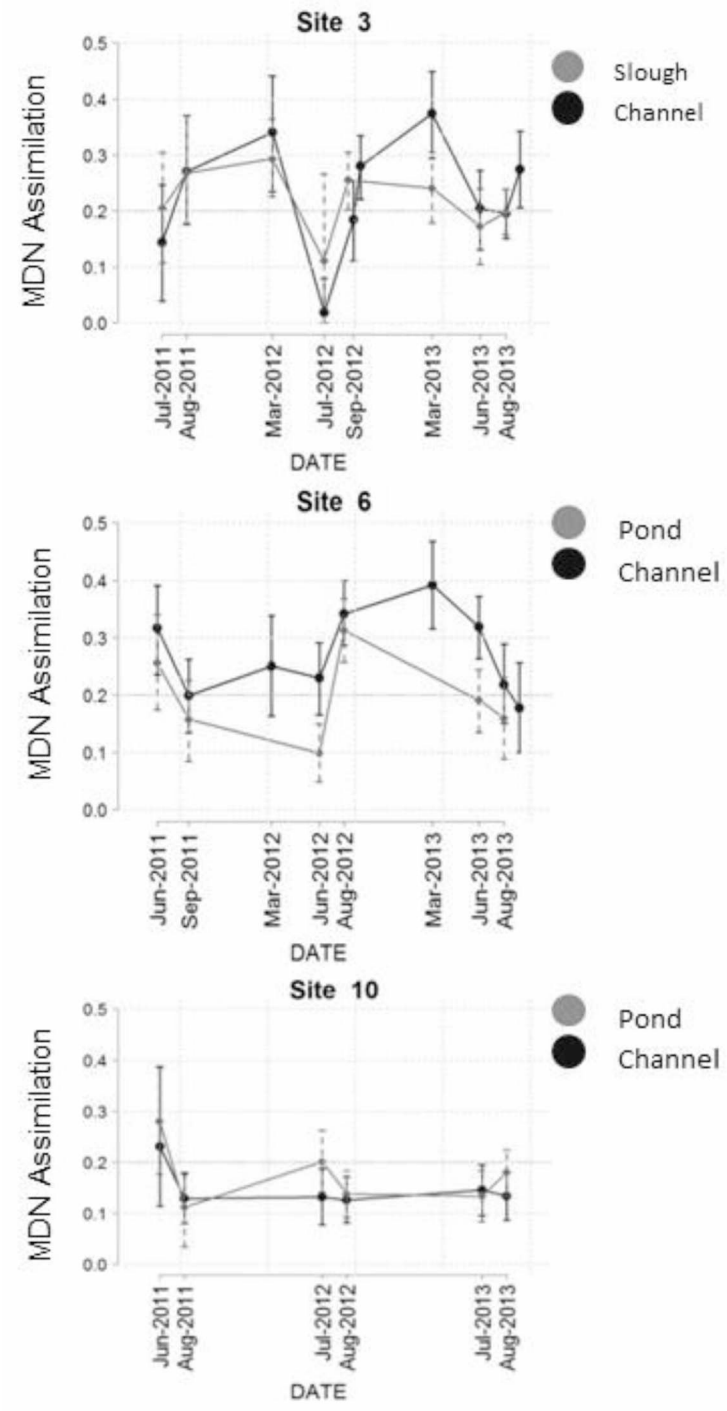

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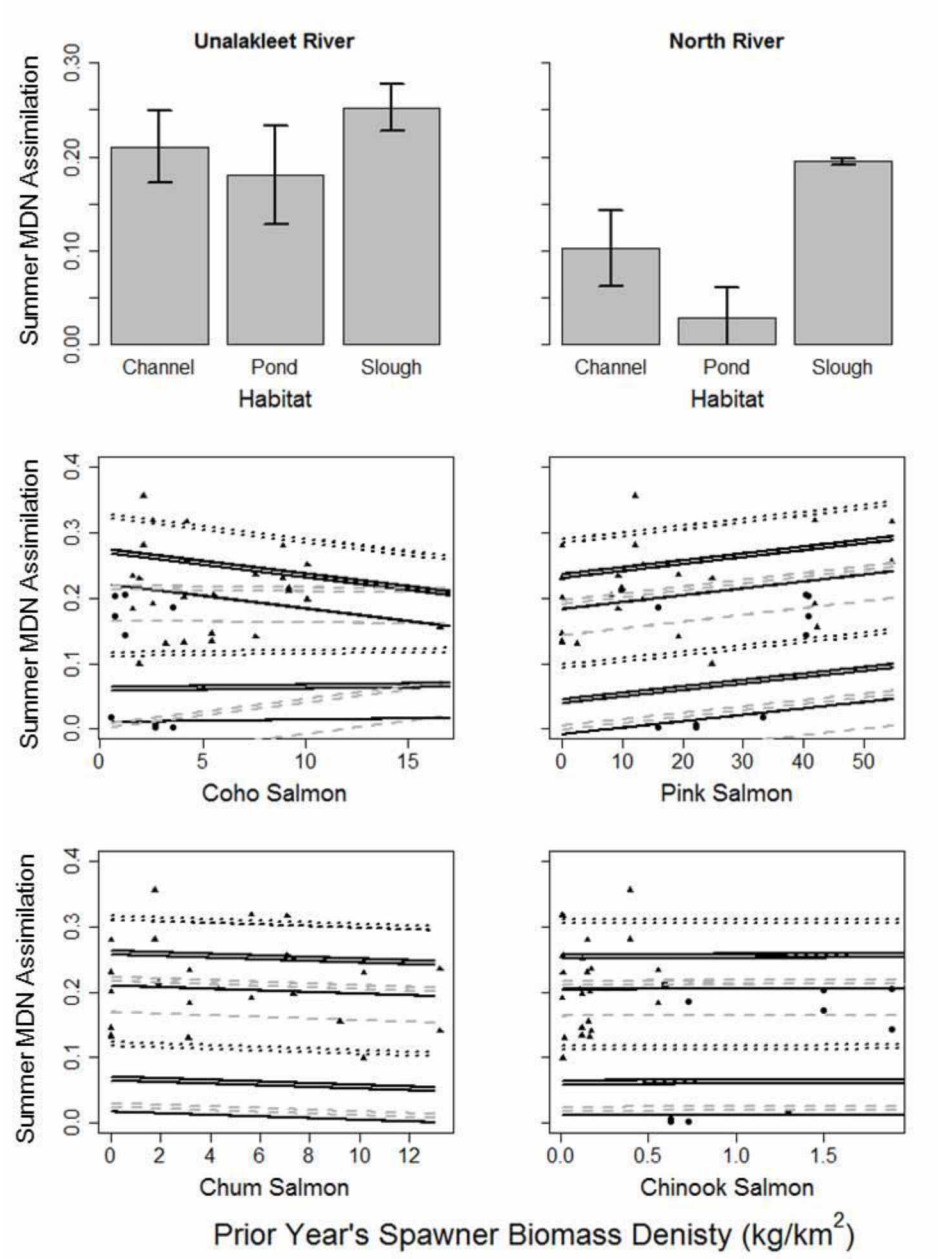

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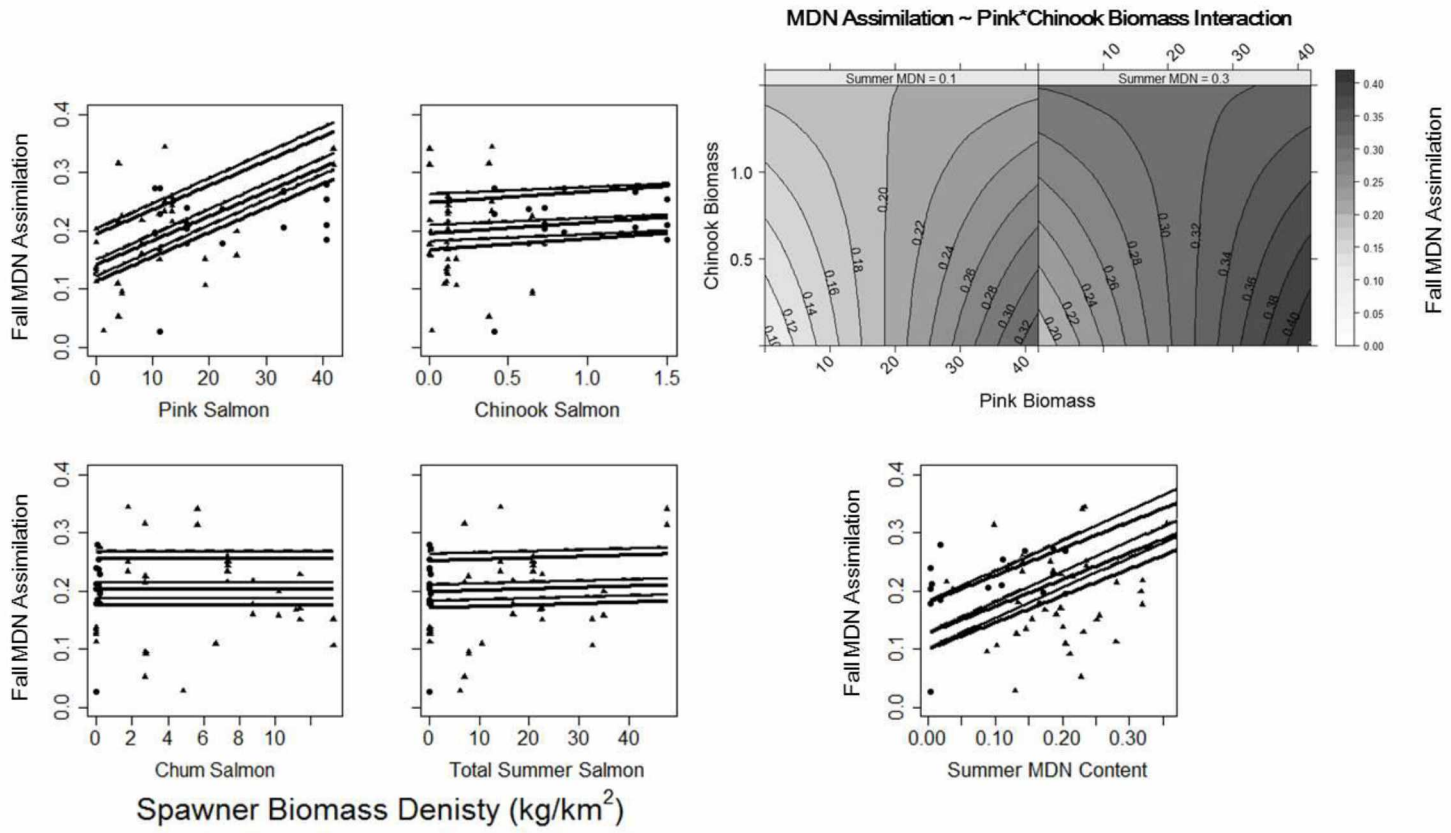

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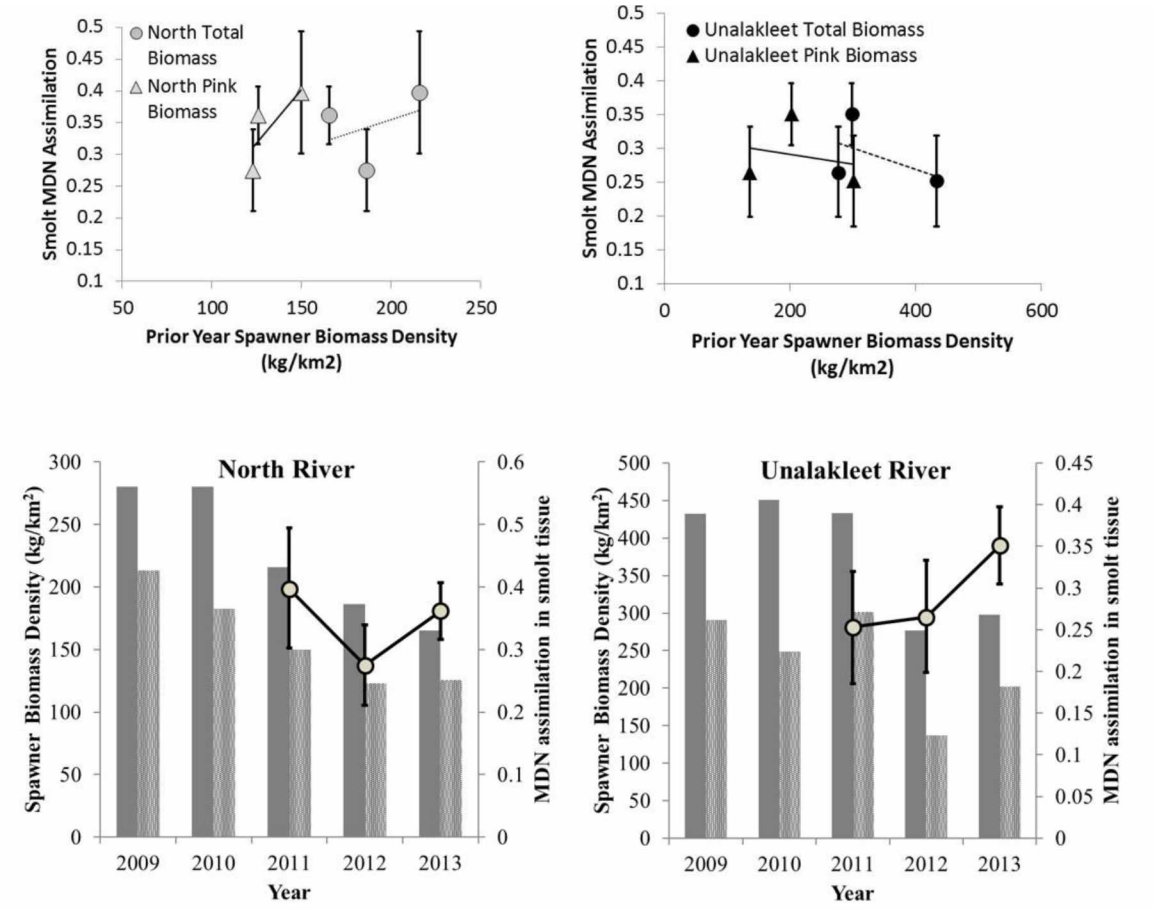

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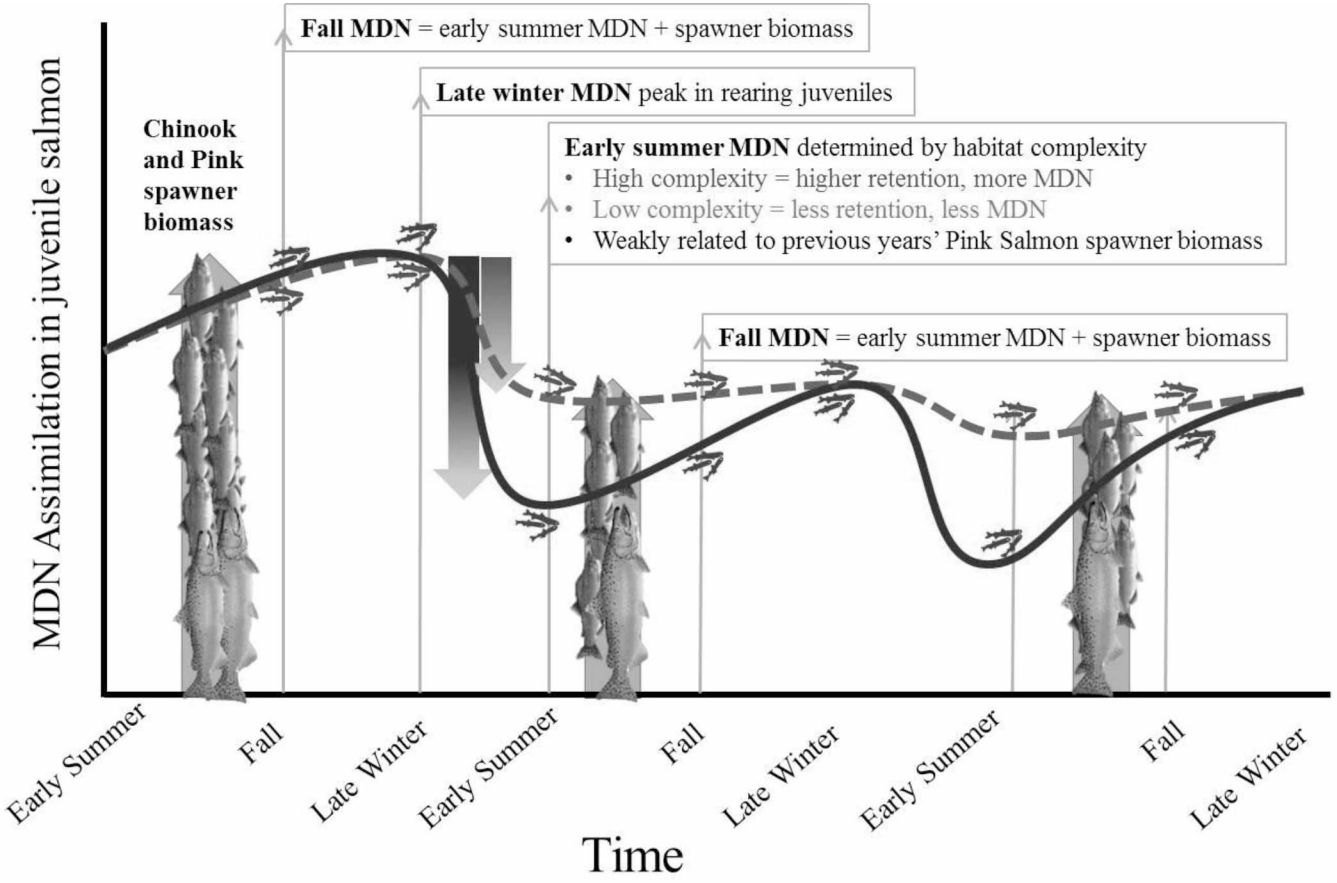

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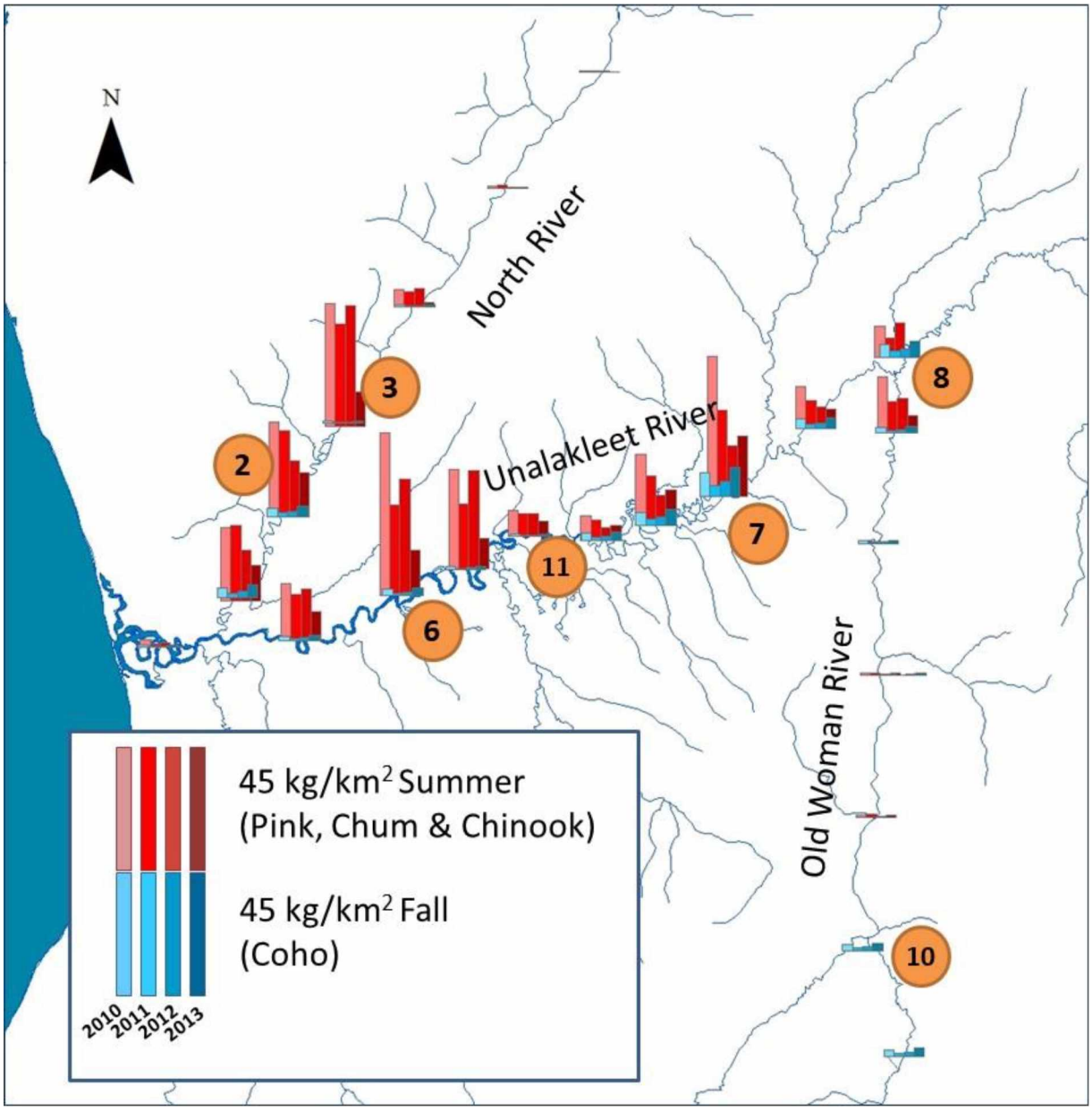
Appendix 2.A.1. Escapements, spawner biomass density, proportion of biomass and contrast (maximum/minimum value) by Pacific salmon species in the Unalakleet River watershed above the Unalakleet River weir and in the North River above the North River counting tower in 2010–2013.

Year	River	Escapement				Biomass Density (kg/km^2)						% Summer Biomass		% Total Biomass
		Pink	Chum	Chinook	Coho[a]	Pink	Chum	Chinook	Summer (Pink + Chum + Chinook)	Coho	Year Total	% Pink	% Chum	% Coho
2010	Unalakleet	832,904	70,811	1,021	52,773	302	81	1.8	385	50	435	78%	21%	11%
2011		393,906	110,731	1,122	25,138	137	116	2.0	255	23	278	54%	45%	8%
2012		680,070	71,593	804	37,048	203	65	1.4	269	30	299	76%	24%	10%
2013		144,225	113,953	767	64,502	52	100	1.4	153	61	214	34%	65%	28%
Contrast ('11-'13)		4.72	1.59	1.46	2.57	3.90	1.78	1.43	1.76	2.65	1.40			
2010	North	150,807	16,131	1,256	7,608	162	42	6.9	211	22	233	77%	20%	9%
2011		123,892	19,898	864	3,624	134	54	4.8	193	10	203	70%	28%	5%
2012		147,674	9,120	996	3,258	137	24	5.5	167	14	181	82%	14%	8%
2013		46,668	10,518	564	8,834	52	28	3.1	83	27	110	63%	36%	25%
Contrast ('11-'13)		3.16	2.18	1.77	2.71	2.63	2.25	1.77	2.32	2.70	1.84			

[a] Because the Unalakleet River weir does not operate through the entirety of the coho salmon run, escapement estimates for Unalakleet River coho salmon were expanded from the North River counting tower by a factor of 6.9 based on radio-telemetry data (Joy and Reed 2007). While this added uncertainty to the analysis, coho salmon spawner abundance was expected to trend similarly between the mainstem Unalakleet and North Rivers (Joy and Reed 2007) and, coho salmon biomass represented less than 12% of total annual spawner biomass.



Appendix 2.A.2. Spawner biomass density for each 10 km section of river for 2010 – 2013 and the location of sampling sites (stars, numbered for reference) in the Unalakleet River drainage. The height of bars represents the biomass (kg/km^2) for summer biomass (red bars) and fall biomass (blue bars) for each 10 km section of river. Sumer biomass represents combined pink, chum and Chinook biomass while fall biomass represent coho salmon biomass.

Chapter 3: Juvenile Coho and Chinook salmon growth, size, and condition linked to watershed-scale salmon spawner abundance

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Juvenile Coho and Chinook salmon growth, size, and condition linked to watershed-scale salmon spawner abundance

Short Title: Spawner abundance and juvenile salmon performance

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MANUSCRIPT HIGHLIGHTS

- Prior to salmon spawning, residual MDN offered little benefit to juvenile salmon.
- After adult spawning, MDN led to increased growth, size and condition in juveniles.
- Benefits to juvenile salmon were related to drainage-wide spawner abundance.

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ABSTRACT

Resource subsidies from spawning salmon (marine-derived nutrients, or MDN) benefit juvenile salmonids while they rear in fresh water, but it is unclear how watershed-scale spawner abundance affects juvenile salmon populations. To address this, we examined juvenile Coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon growth, size, condition, and abundance as a function of MDN use. MDN assimilation in juvenile salmon was tracked with stable isotopes, growth rates were assessed using RNA:DNA ratios, a mixing model was used to estimate age-specific mean lengths, and Ricker's condition factor was used to assess body condition. A mark-recapture experiment provided abundance estimates of Coho Salmon smolts emigrating from the Unalakleet and North rivers, western Alaska, USA. Prior to salmon spawning, residual MDN from past years offered little advantage to juvenile salmon. However, after the arrival of spawning salmon, juvenile salmon demonstrated a positive relationship between MDN and fish size, growth, and condition in fall and winter. Outmigrating smolts also benefitted from MDN resources via increased size and growth. Coho Salmon smolt abundance was unrelated to total spawner biomass, but a positive relationship between MDN assimilation and smolt abundance suggested a possible effect on over-winter survival. Furthermore, similar trends in spawner biomass and the abundance of age-1 smolt suggested that age-at-smolting was influenced by MDN. These relationships suggest that spawner abundance during Coho and Chinook salmon rearing is an important factor in the juvenile productivity of these species.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) accumulate over 99% of their adult mass while growing at sea and transport significant quantities of marine carbon, nitrogen and other nutrients (marine-derived nutrients; MDN) when returning to spawn and die in fresh water. Pulsed marine subsidies increase the quantity and quality of juvenile salmon diets as fish feed directly on large, energy rich diet items such as eggs, carcasses, fry and smolt (Parker 1971; Hargreaves and LeBrasseur 1985; Ruggerone and Rogers 1992; Bilby and others 1998; Pearsons and Fritts 1999; Denton and others 2009; Armstrong and others 2010).

In localized settings, access to marine subsidies has been shown to increase growth rates and improve overall condition, including increasing lipid content in juvenile salmon. Evidence from studies throughout the Pacific Northwest and Alaska has highlighted the benefit of densely spawning adults from species such as Pink (*O. gorbuscha*), Chum (*O. keta*), and Sockeye salmon (*O. nerka*) to juveniles of other salmonid species while they rear in fresh water (Bilby and others 2003; Wipfli and others 2010; Rinella and others 2012). Juvenile Coho Salmon exhibited increased growth (Wipfli and others 2003; 2010) and lipid content (Heintz and others 2004, 2010) in response to Pink Salmon carcasses, and Coho Salmon and Dolly Varden (*Salvelinus malma*) also demonstrated elevated growth rates and energy content with increasing salmon spawning density in Southcentral Alaska streams (Rinella and others 2012). Spawning adult Sockeye Salmon in southwest Alaska have been shown to benefit stream dwelling juvenile salmonids, including Coho Salmon, Dolly Varden, and Rainbow Trout (*O. mykiss*), by increasing ration size, body condition, and growth (Scheurell and others 2007; Denton and others 2009; Armstrong and others 2010).

Factors that enhance juvenile salmon growth, size, lipid reserves, and overall body condition have the potential to ultimately affect overall stock productivity by increasing juvenile survival and smolt production. Salmon stock productivity is frequently described as recruitment to the spawning adult life stage, relative to the number of spawners in the parent generation. In turn, recruitment is largely determined by both the abundance and survival of juveniles (Quinn 2005). Higher freshwater survival

rates ultimately increase smolt abundance and consequently have strong potential to influence productivity (Ebersole and others 2006). Survival of juvenile salmon in fresh water is partially a product of body size and condition as larger fish with greater lipid reserves demonstrate higher survival rates during periods of food shortages, particularly during over-wintering periods (Quinn and Peterson 1996; Zabel and Achord 2004; Brakensiak and Hankin 2007; Pess and others 2011). Fish size also provides competitive advantages as larger fish are less prone to predation (Sogard 1997), less likely to suffer from disturbances such as flooding (Pearsons and others 1992; Bell and others 2001; Pess and others 2011) and are more competitive in defending preferred feeding stations (Ejike and Schreck 1980; Reinhardt 1999; Nielsen 1992; Rosenfeld and Hatfield 2006). In addition to affecting freshwater survival rates, enhanced smolt size may also increase marine survival rates given that size-selective mortality can be particularly strong during the early marine portion of the life cycle (Holtby and others 1990; Beamish and others 2004; Duffy and Beauchamp 2011). Furthermore, juvenile salmon survival is related to lipid stores (often approximated by condition indices) (Biro and others 2004; Rinchard and others 2007) that allow fish to store abundant resources from pulsed subsidies, including MDN, for later use when food is scarce (Heintz and others 2010). Over-winter survival rates are directly related to lipid reserves (Post and Parkinson 2001; Biro and others 2004; Finstad and others 2004; Rinchard and others 2007) and freshwater productivity is thought to be partially limited by the quality of energetic resources (Cunjak and others 1996, 1998; Bradford and others 1997; Ebersole and others 2006).

Despite a large body of literature documenting the benefit of MDN to juvenile salmon growth and condition in experimental settings or at relatively small scales, there has been limited research scaling up these findings to the population and watershed level, leaving a gap in our understanding of the response of juvenile salmon stocks to the abundance of spawning adult salmon within a watershed (Piccolo and others 2009; Bernard and Clark 2009). Given how MDN has been shown to improve juvenile salmon growth and condition, it is reasonable to hypothesize that these effects ultimately influence stock productivity. Indeed, juvenile abundance was indirectly associated with MDN in British Columbia where juvenile

Coho Salmon abundance was positively related to adult Pink Salmon abundance (Nelson and Reynolds 2014). In western Alaska, correlations between spawner abundance and returns of Pink and Coho salmon were best explained by Pink Salmon marine subsidies improving Coho Salmon productivity (Joy and others *in prep*[b]). Moreover, this work demonstrated that MDN use by juvenile Chinook and Coho salmon in western Alaska was a function of Pink and Chinook salmon distribution and abundance (Joy and others *in prep*[a]). However, while demonstrating these relationships, the effects on factors affecting stock productivity, such as juvenile salmon growth, condition, and abundance were not examined.

The goal of this project was to assess the relationship between adult spawner abundance and juvenile salmon performance metrics that in turn affect salmon productivity. Our objectives were to determine if juvenile salmon growth rates, size, and condition (weight: length relationships) were related to MDN assimilation and to examine Coho Salmon smolt abundance and age distribution in relation to MDN assimilation and spawner abundance. To better understand how these relationships would affect watershed-scale productivity we accounted for the demographics of the juvenile Coho Salmon population, examined these relationships relative to channel and off-channel habitat use, and accounted for environmental variables, such as water temperature and river depth, which may also impact juvenile salmon performance metrics (growth, size, and condition). We examined two sub-drainages in the Unalakleet River watershed on a seasonal basis by sampling out-migrating smolt in the spring and rearing parr early in the summer, before the arrival of spawning salmon, and in the fall after salmon had spawned. Within those sampling periods, we compared juvenile salmon size, growth and condition to MDN assimilation in juvenile salmon while factoring in explanatory variables and interactions including habitat, fish size and age, water temperature, and river depth.

METHODS

Study area: The Unalakleet River drains approximately 4,800 km^2 of the Nulato Hills into the eastern end of Norton Sound on the west coast of Alaska (63.878°N, 160.605°W) (Figure 1). The North River is the largest tributary and the confluence occurs 7.2 km above the Unalakleet River mouth (Figure 1). The

North River is characterized by a narrow valley with low sinuosity and minimal off-channel habitat while the Unalakleet River is characterized by a broad, u-shaped valley with greater sinuosity and large amounts of off-channel habitat such as sloughs and ox-bows (Figure 3.1).

The watershed supports populations of Chinook, Coho, Chum, Pink, and Sockeye salmon. Escapements are monitored annually on the North River with a counting tower and on the Unalakleet River (above its confluence with the North River) with a weir (Menard and others 2013). In terms of biomass, Pink Salmon are the dominant species in the system (5 year average of 67 and 54% of biomass in North and Unalakleet rivers, respectively), followed by Chum (17 and 34%) and Coho salmon (14 and 11%). Chinook Salmon constitute 3 and 0.6% of the annual anadromous biomass imported to the North and Unalakleet river watersheds while the Sockeye Salmon biomass is trivial (Menard and others 2013). Pink, Chum, and Chinook salmon begin their spawning migration in late June and have finished spawning by early August. Coho Salmon spawn in September and October (Menard and others 2013).

Juvenile sampling: To estimate MDN assimilation in juvenile salmon tissue as well as estimate growth rates, condition factor, size, and age, fish were sampled in 2011 – 2013 before (summer) and after (fall) the arrival of spawning salmon, in late winter (March), and during the spring smolt migration (May and June) (Appendix 3.A.1). Early summer (June 12 – July 12), mid-summer (July 28 – August 6), mid-fall (August 22 – September 12), late fall (September 20 – October 5), and winter (March 4 – 14) sampling of rearing Chinook and Coho salmon (hereafter referred to as parr) occurred at sampling sites distributed throughout the watershed (Figure 3.1). At each site, parr were sampled in main-channel and off-channel habitats. Sampling of channel habitat occurred amongst woody debris along cut banks. Off-channel sampling occurred in lentic water bodies that were either an open-mouth slough (sites 3, 7, and 8) or a pond with minimal connectivity to the mainstem (sites 2, 6, and 10). Parr were sampled by soaking baited minnow traps for two hours and approximately 15 fish per species and habitat type (channel or off-channel) were sampled during each event for stable isotopes and R/D samples. Up to 200 more fish were

sampled for length. Winter samples were taken from a subset of locations (Sites 2, 3, 6, and 8), in March 2012 and 2013, by fishing minnow traps through holes in the ice.

For Chinook and Coho salmon smolts, samples were obtained from fifty smolt of each species captured in the lower end of the North and Unalakleet rivers (above their confluence) (Figure 3.1) over the course of the smolt migration (mid-May, depending on ice-out, to July 1) in a fyke trap (North River; 1.2 m high by 1.5 m wide) and a 2.4 m diameter rotary screw trap (EG Solutions, Corvallis, OR) (Unalakleet River).

Sampled fish were anaesthetized using diluted clove oil solutions (20 υl clove oil/L water) (Cho and Heath 2000), identified to species, measured to the nearest mm (fork length), and weighed to the nearest 0.1 g. A caudal fin clip (<0.25 cm^2) was excised and frozen for stable isotope analysis (Sanderson and others 2009; Hanisch and others 2010). To age Coho Salmon, scales were sampled in 2012 and 2013 using a curved scalpel blade swiped along the preferred region (above the lateral line and behind the dorsal fin) and stored on glass slides (Scarnecchia 1979). To estimate R/D, a 1–3-mm-long tissue sample was taken from the muscle lateral to the dorsal fin using a 2-mm-diameter biopsy punch, placed in a RNA preserving buffer (RNALater, ThermoFisher Scientific, Grand Island, NY), and frozen (Calderone and others 2001; Maclean and others 2008). In 2012 and 2013, Coho Salmon were euthanized with an overdose of clove oil and frozen so as to determine dry weights after desiccation in the lab. All Chinook Salmon and Coho Salmon in 2011 were released after recovery from anesthetic.

Fish aging: Juvenile Coho Salmon were aged by identifying and counting annuli on scale samples magnified with a microfiche reader. Coho Salmon were aged as age-0 (fish that emerged that spring, had not overwintered and had no annuli), age-1 (fish that overwintered in fresh water after emergence), age-2 or age-3 depending on the number of annuli present (Mosher 1969; Campana 2001). For analysis, rearing parr were examined as two age classes; age-0 and age-1+, which refers to parr of age-1 and -2. Smolt were also examined as two age classes; age-1 and age-2+, which refers to both age-2 and age-3 smolt. It was unnecessary to age Chinook Salmon given that >99% of Norton Sound Chinook Salmon smolt after one year in fresh water (Menard and others 2013).

Stable isotope analysis and MDN assimilation in fish tissue: MDN assimilation was estimated in individual fish and fish populations at sampling sites using stable isotopes of C and N and mixing models that compared fish stable isotope ratios to samples representing minimal MDN sources and marine samples such as adult salmon flesh, eggs and fry samples. Stable isotopes $\delta^{15}N$ and $\delta^{13}C$ values of marine organic material are typically higher than those in terrestrial and freshwater environments (Bilby and others 1998, Chaloner and others 2002; Wipfli and others 2003) and since spawning salmon cease feeding in fresh water, they retain marine signatures which can thus be used to trace MDN through freshwater ecosystems (Chaloner and others 2002). The stable isotope signatures of juvenile salmon were obtained from fin clips (Sanderson and others 2009; Hanisch and others 2010) and detailed methodology for laboratory and analytical procedures are covered in Joy and others (*in prep*[a]). We used MixSIAR, a Bayesian mixing model (Moore and Semmens 2008; Stock and Semmens 2013), to estimate MDN assimilation in individual juvenile salmon (individual MDN assimilation) and the population of fish at sampling sites (site MDN assimilation) such that site MDN assimilation was the Bayesian average of the individuals at that site.

RNA:DNA analysis: Nucleic acid levels (R/D) in juvenile salmon muscle tissue were measured using a fluorescence-based assay (Caldarone and others 2001). While the amount of DNA in a given cell is fixed, the amount of RNA present is directly related to the amount of protein synthesis. R/D in muscle cells have proved to be a useful index of specific growth rates directly linked to recent somatic growth (Wang and others 1993; MacLean and others 2008; Caldarone and others 2011). Caldarone and others's (2001) methods were modified such that frozen muscle plug samples preserved in RNAlater were thawed and homogenized in 500 µL 0.1% STEB (one g N-Lauroylsarcosine sodium salt (Sigma Cat # L9150) dissolved in 100 mL TE buffer) with 0.25 mL 1 mm zircona beads (BioSpec Products Cat # 11079110zx) in a Precellys 24 bead-beating homogenizer at 6,000 K for 20 seconds. GelGreen nucleic acid staining dye (Biotium Cat # 41005) was used in lieu of Ethidium Bromide.

In 2011, the commercial purified RNA used in Caldarone and others (2001) was no longer available and there were no other sources available. Instead RNA was purified from lab-maintained blacktail shiner (*Cyprinella venusta*) and used as standard. Muscle tissue was homogenized in Tri Reagent (Molecular Research Center Cat # TR118) and the RNA isolated using Direct-zol RNA MiniPrep column purification (Zymo Research Cat # R2050) according to the manufacturer's protocol. Any contaminating DNA was digested and removed using TURBO DNA-free reagent (Life Technologies Cat # AM1907M). The concentration of purified RNA was quantified by UV absorbance based on the extinction coefficient of RNA and one OD_{260} = 40 ug/mL. In 2012, a new commercially available RNA standard named RiboReady I Kb RNA ladder (Amresco Cat # N604) was used. In 2013, RiboReady RNA was removed from the market, so we used the RNA standard in the Promega QuantiFluor RNA System (Promega Cat # E3310). Replicate RNA readings varied by ±7% in 2011, 4% in 2012 and 9% in 2013 while DNA replicates varied by ±3% in 2011 and 2012 and by 2% in 2013.

Body condition: Fish condition was assessed using Ricker's Condition Factor (Bolger and Connolly 1989) which compares the length:weight relationship of the individual to that of the population and corrects for the correlation between length and condition present in other condition factors (Herbinger and Friars 1991; Sutton and others 2000; Hanson and others 2010). Condition was determined from Chinook Salmon wet weights (K_{wet}) and Coho Salmon dry weights (K_{dry}). Condition indices derived from dry weights were preferable as fish simultaneously lose water weight while increasing lipid reserves prior to winter (Sutton and others 2000). However, due to political and conservation concerns expressed by local residents, we did not sacrifice Chinook Salmon. To dry Coho Salmon, bodies were desiccated for 72 hours in a drying oven (60°C) after which fish were weighed to the nearest 0.01 g. Ricker's condition factor, K, was calculated as

$$K = \frac{W}{L^b} (1)$$

where W was the weight (wet or dry) of the fish in grams, L the length in mm and b the parameter of the regression of log10 weight on log10 length (Bolger and Connolly 1989). The b parameter was derived using all measured and weighed fish from each species over the course of the study.

Mean length and age composition of Coho Salmon parr: To determine the mean lengths and population proportions of age-0 and age-1+ Coho Salmon (age distribution) at each sampling site for each sampling period, a Bayesian mixture model (Lynch 2007) was employed utilizing the length frequency distributions of Coho Salmon and known ages. The probability density function (pdf) of measured fish length (y) was modeled using a weighted mixture model:

$$f(y) = p_1 f_1(y) + p_2 f_2(y) \tag{2}$$

$$0 \leq p_1, p_2 \leq 1$$

where $f_1(y)$ was the length distribution of age-0 and $f_2(y)$ was the length distribution of age-1+; weights p_1 and p_2 were the proportions parameters of the age-0 and age-1+, respectively, so that $p_1 + p_2 = 1$.

Length distributions $f_1(y)$ and $f_2(y)$ were assumed to be normally distributed and the mixture model was fitted via a Bayesian approach, implemented by Markov Chain Monte Carlo (MCMC) using the statistical program JAGS (Plummer 2003) and R (R Core Team 2013). A non-informative Dirichlet distribution was used as priors for age classes (p) and a non-informative normal distribution was used for the mean length (and standard deviation) of each age class. After model fitting, the means and standard deviations of age class proportion p_1 and p_2, together with the mean length and associated standard deviation of both age classes were calculated. Chains were run three times to assess convergence.

Smolt abundance estimation: The number of Coho Salmon smolt emigrating from the North River and the mainstem Unalakleet River above its confluence with the North River (Figure 3.1) in 2011–2013 was estimated using a two-event mark-recapture experiment for a closed population (Seber 1982). This experiment was designed to accommodate varying capture probabilities over the course of the smolt migration such that a temporally stratified estimator could be used to estimate abundance (Darroch 1961;

Arnason and others 1996). The marking event occurred when emigrating smolt were captured as they migrated down river, marked and subsequently released up river of sampling gear. The recapture event occurred when smolts were recaptured as they passed through the sampling area a second time and were captured in either a different set of gear (2011) or a subset of the gear used in the marking event (2012 and 2013). In 2011, fish captured in minnow traps constituted the marking event and fish captured in a second series of minnow traps in the North River and a rotary screw trap in the Unalakleet River constituted the recapture event. To increase sample sizes in 2012 and 2013, fish captured in all gear (including a fyke trap in the North River, the Unalakleet river screw trap and minnow traps in both rivers) were marked while the fyke trap and screw trap served as the recapture event. During the mark and recapture events, minnow traps baited with salmon roe were fished in the North River in a 3-km section of river extending upriver from the counting tower and in the Unalakleet River between 4 and 7 km upriver from the confluence of the North and Unalakleet rivers (Figure 3.1). The rotary screw trap was fished in the Unalakleet River 3.6 km above its confluence with the North River, and the fyke trap was fished at the North River counting tower (Figure 3.1). Fish captured in minnow traps were double marked with Bismark Brown Y dye (50 mg dye/L water; Sigma-Aldrich CAS# 10114-58-6) and a colored tattoo on the caudal fin using a Micro-JECT injector (New West Technologies, Santa Rosa, CA) (Dietrich and Cunjak 2006). In 2012 and 2013, fish captured in the rotary screw trap (Unalakleet River) and fyke trap (North River) were also double marked with dye and a fin notch, thus allowing us to determine if capture probabilities varied by capture gear. The color of the tattoo and shape of the fin notch were changed every three days to examine how capture probabilities varied over time. To determine how capture probabilities varied by fish size, we measured fish fork length (mm) from 200 fish captured in minnow traps, fyke traps, and screw traps each day in addition to measuring every recaptured (previously marked) fish.

The mark-recapture experiment was designed to ensure that assumptions of population closure were not violated, handling effects were minimized, and appropriate diagnostic tests were performed to identify

variability in capture probabilities based on fork length, capture gear, and sampling period (Seber 1982; Appendix 3.A). When diagnostic tests indicated variability in capture probabilities, data were stratified by fish length, capture gear, and/or temporal periods such that capture probabilities did not vary significantly within strata. Once appropriate size strata were identified with diagnostics, a temporally (and gear, if necessary) stratified abundance estimator (Darroch 1961) was used to estimate abundance. The computer program SPAS (Arnason and others 1996) was used to calculate maximum-likelihood abundance estimates and their associated variance. The number of temporal categories for each sampling event as determined by diagnostic tests was sometimes further reduced to produce matrices that yielded valid abundance estimates (Arnason and others 1996). The proportion of age-1 and age-2+ Coho Salmon smolt was estimated from aged scales and abundance estimates for the two age classes calculated from total smolt abundance in the North and Unalakleet river populations.

Data analysis and MDN effects on juvenile salmon performance metrics: To determine if juvenile salmon growth (R/D), condition (*K*), and size (individual fish length, and mean population length) varied in relation to MDN assimilation and other biological and environmental variables, we used mixed effects generalized linear models (GLMM) (Stroup 2012) and multi-model inference to estimate the importance and effect of variables (Burnham and Anderson 2002; Calcagno and Mazancourt 2010). To examine how R/D, *K*, and fork length varied as a function of MDN assimilation, we examined within-season variation in these metrics. For each species (Coho and Chinook salmon) and season (summer, fall, winter and spring/smolt), the response variable of interest (all with normal error distributions) was fit to GLMMs where year and sampling site were set as random effects to control for pseudoreplication. Fixed effects included river (North or Unalakleet mainstem), habitat type (channel, slough or pond), river size (watershed area above the sampling location in km^2), site MDN assimilation, individual MDN assimilation, water temperature, and river depth. Fish length was also included as an explanatory variable when analyzing R/D and *K*. To avoid issues of collinearity, individual MDN assimilation was analyzed relative to site MDN assimilation (i.e., as the difference between individual and site MDN assimilation).

Collinearity in other variables was not identified in our data set given that Pearson's R^2 values never exceeded 0.15 (Booth and others 1994; Dormann and others 2012). All numerical effects were standardized to aid algorithms in identifying maximum likelihood estimates.

Water temperature and depth were modeled as follows. Water temperature was recorded daily at the North River counting tower and Unalakleet River weir sites from early-May to late-September and temperature from the two sites was used for the study sites located within the respective sub-drainages. For summer sampling periods, the average daily temperature between ice-out and the summer sampling date was used. For fall sampling periods, the average daily temperature between the summer and fall sampling periods was used. To examine how smolt performance metrics were affected by the prior years' growing season, temperature was modelled in the spring analysis as the average daily river temperature from the previous year. River depth was taken from the daily recordings of the gauge at the North River counting tower and summer and fall values calculated similarly to temperature variables.

For each analysis (summer and fall), a global model and subsets of models were examined to determine the most relevant explanatory variables. Akaike's Information Criterion adjusted for small sample size, AICc (Burnham and Anderson 2002), was used to rank and weight possible models nested within the global model using the glmulti (Calcagno and Mazancourt 2010) and the MuMIn packages (Barton 2016) in the statistical platform R (R Core Team 2013). We examined all possible combinations of factors and interactions while limiting model size to seven total parameters. Following the rule of marginality, interactions were only included in a model if both of the main effects in the interaction were also included. Factors and interactions were examined for their effect on the response variable using the relative evidence weight, importance (I), computed as the sum of the relative evidence weights in which the term appeared. A threshold importance of 80% was used to denote "significance" (Calcagno and Mazancourt 2010; Galipaud and others 2014). Model-averaged results were used to predict the effect of MDN on the variable of interest (R/D, K, fork length, and mean fork length) while holding other variables constant. Because it is not possible to place confidence intervals on predicted values from coefficients

averaged across GLMMs, we predicted values for each site and year (the random effects) and used I to gauge significance. We presented plots of predicted values as the average and standard deviation of the predicted values derived from the range of random effects (sampling site and year). Only significant results are presented in the results while insignificant results are presented in the appendices.

To gauge the amount of variability in each analysis derived from MDN effects alone, we calculated the marginal R^2 score from the model containing the two MDN variables (site and individual), significant interactions involving MDN variables (but excluding non-MDN terms, thus ignoring the marginality rule in this case) and the random effects of year and sampling site (Madsen and others 2011; Stroup 2012; Galipaud and others 2014). This R^2 score is referred to as MDNR^2.

To examine how MDN related to Coho Salmon smolt abundance, we compared smolt abundance to smolt MDN assimilation and spawner biomass density in the previous year, as calculated in Joy and others (*in prep*[a]). Given only three years of data and two rivers, these results were examined qualitatively and in light of how performance metrics (R/D, K, fork length, and mean fork length) related to MDN use by juvenile salmon.

RESULTS

Pre-spawner MDN and performance metrics (size, growth, condition) of early summer parr: Prior to the migration of spawning salmon into the watershed, residual MDN derived from the previous year was positively related to some juvenile salmon metrics, but negatively related to others. Chinook Salmon growth, size, and condition were unrelated to MDN on any scale ($I < 0.27$ in all cases) while Coho Salmon demonstrated variable relationships with residual MDN, dependent on age and habitat (Figure 3.2, Appendix 3.B.1 and B.2). Overall, Coho Salmon demonstrated a significant, positive relationship between R/D and site MDN assimilation, but the amount of variability in summer R/D explained was very small (MDN$R^2 = 0.0091$). Coho Salmon also exhibited a positive relationship between fork length and individual MDN assimilation in the summer (MDN$R^2 = 0.083$) that was evident in age-1+ Coho Salmon (MDN$R^2 = 0.058$) but absent in age-0 fish. In contrast, the strongest relationship with pre-

spawner MDN was a negative relationship between condition, *K*, and both site and individual MDN assimilation (MDNR^2 = 0.29). By age class, age-0 Coho Salmon showed a significant, negative relationship between *K* and individual MDN assimilation (MDNR^2 = 0.53) while age-1+ fish demonstrated a negative relationship between *K* and site MDN assimilation (MDNR^2 = 0.32).

Post-spawner MDN and fall parr: After spawning migrations of Pink, Chum, and Chinook salmon, fall juvenile Chinook Salmon had a positive relationship between fork length and site MDN assimilation, although there was considerable variability due to the random variables of sampling site and year (Figure 3.3 and Appendix 3.B.3 and B.4). However, there was a strong relationship between individual MDN assimilation and fork length (MDNR^2 = 0.28) and a modest, positive relationship between Chinook Salmon condition, *K*, and site MDN assimilation (MDNR^2 = 0.091) (Figure 3.3).

Coho Salmon also demonstrated similar relationships between fork length, *K*, and both site and individual MDN assimilation (MDNR^2 = 0.16 and 0.12 for fork length and *K*, respectively; Figure 3.4). The relationship between site MDN assimilation and *K* was only present in age-1+ fish (MDNR^2 = 0.38). The relationship between fork length and site MDN also was present only in age-1+ fish, but differed from the total Coho Salmon population in relation to habitat. Age-1+ Coho Salmon demonstrated a positive relationship between fork length and site MDN in pond and channel habitats, but were negatively related in slough habitat (MDNR^2 = 0.052). The relationship between fork length and individual MDN assimilation present in all Coho Salmon was similar, but less significant in age-1+ fish (Figure 3.4). In age-0 fish, there was a significant relationship between individual MDN assimilation and fork length that was positive in channel habitat, slightly positive in pond habitat, and negative in slough habitat (MDNR^2 = 0.15).

Bayesian analysis of the mean fork length of each age class demonstrated that age-0 Coho Salmon was positively related to site MDN assimilation in the mainstem Unalakleet River, but negative in the North River tributary (Figure 3.4; MDNR^2 = 0.22). Mean fork length of age-1+ Coho Salmon was positively related to site MDN assimilation in both rivers (MDNR^2 = 0.078).

Coho Salmon also demonstrated a significant relationship between R/D and site MDN assimilation (MDNR^2 = 0.12) that was strongest in age-1+ Coho Salmon (MDNR^2 = 0.12) and absent in age-0 fish (Figure 3.4). The relationship was positive in pond and slough habitat, but negative in channel habitat.

MDN and overwintering Coho Salmon: Overwintering Coho Salmon demonstrated a strong, positive response to MDN assimilation at both the individual and site level (Figure 3.5 and Appendix 3.B.5). Fish exhibited higher *K* indices at high MDN sites and fish with high individual MDN assimilation were larger (fork length, MDNR^2 = 0.22) and in better condition (*K* indices, MDNR^2 = 0.30). *K* indices were highest in larger fish with high individual MDN assimilation as indicated by a positive interaction between length and individual MDN assimilation (Figure 3.5).

MDN and water depth interactions: Several analyses suggested that the effects of MDN on Coho Salmon performance metrics were dependent on water depth (as measured at the North River counting tower) in the fall (Figure 3.6). Interactions between water depth and individual MDN assimilation show the relationship between individual MDN assimilation and fork length increased with increasing water depth (Figure 3.6). Furthermore, the interaction between site MDN assimilation and water depth also had a notable influence on fall R/D (Figure 3.6). In channel habitat, the negative R/D ~ site MDN relationship weakened with increasing depth. In sloughs and ponds, the positive relationship increased in strength with increasing depth.

MDN and out-migrating smolt: Performance metrics in outmigrating Coho Salmon smolt were positively related to individual MDN assimilation, but negatively related to site MDN assimilation. Coho Salmon smolt fork length was negatively related to site MDN assimilation, but positively related to individual MDN assimilation in Unalakleet River smolt (Figure 3.7 and Appendix 3.B.6; MDNR^2 = 0.16). Condition, *K*, demonstrated a similar pattern with a strongly negative relationship between *K* and site MDN assimilation and a slight, but significant, positive relationship to individual MDN assimilation (Figure 3.7; MDNR^2 = 0.15). R/D in Coho Salmon smolt were not significantly related to MDN assimilation.

Chinook Salmon smolt demonstrated more positive associations between performance metrics and MDN than did Coho Salmon. Most notably, Chinook salmon R/D were positively related to site MDN and there was a weak and slightly negative relationship to individual MDN assimilation (Figure 3.7; MDNR^2 = 0.084). Chinook Salmon smolt lengths were also positively related to individual MDN assimilation (MDNR^2 = 0.087), but *K* indices were negatively related to site MDN assimilation (MDNR^2 = 0.13).

Smolt abundance: Coho Salmon smolt abundance in the North and mainstem Unalakleet rivers (Table 3.1) did not trend in accordance with declining spawner biomass (Figure 3.8), but there were similar trends in the North River between spawner biomass, smolt MDN assimilation and smolt abundance that were either less apparent or entirely absent in Unalakleet River smolt. Qualitative examination of smolt data revealed a negative relationship between spawner biomass and smolt abundance in the Unalakleet River that was mirrored in the abundance of age-2+ smolts while the abundance of age-1 smolt remained constant (Figure 3.8.A). In the North River, there was a positive trend between smolt abundance and spawner biomass. That positive trend was more direct in age-1 smolts, particularly when compared to Pink Salmon biomass (Figure 3.8.A). Juxtaposed to this was a negative trend between spawner biomass and the abundance of age-2+ smolts (Figure 3.8.A).

The stronger apparent relationship between spawner biomass and smolt abundance in the North River (Figure 3.8.A) also was evident when examining the relationship between spawner biomass and smolt MDN assimilation (Figure 3.8.B) and the subsequent relationship between smolt MDN assimilation and smolt abundance (Figure 3.8.C). Spawner biomass in the previous year trended similarly with smolt MDN assimilation in the North River, particularly with regard to Pink Salmon biomass, while the relationship was weakly negative in the Unalakleet River (Figure 3.8.B; Joy and others *in prep*[a]). Subsequently, the relationship between smolt MDN assimilation and smolt abundance trended very similarly in the North River, but not so in the mainstem Unalakleet River (Figure 3.8.C).

DISCUSSION

Summary of annual MDN benefits to rearing juveniles: Our results demonstrated how MDN benefits to juvenile salmon documented in previously published smaller scale studies were evident at a watershed scale and, coupled with Joy and others (*in prep*[a]), related to drainage-wide spawner abundance. MDN benefitted juvenile salmon to some extent in all seasons in the form of increased size, higher growth rates, and better condition (Figure 3.9) and a consistent association between MDN assimilation and fish length in all seasons suggested marine subsidies were a critical resource to growing fish. Residual MDN was weakly associated with larger size and higher growth rates (particularly in off-channel habitat) but was associated with noticeably lower condition indices (*K*). Following salmon spawning migrations, fall MDN assimilation in juvenile salmon was associated with larger size, better condition, and higher growth rates. These benefits were even more dramatic in late winter as MDN was strongly associated with greater size and better condition. In the spring, MDN offered limited benefits to outmigrating Coho Salmon smolt, but substantial benefit to outmigrating Chinook Salmon smolt in the form of higher growth rates and bigger size. Thus, while residual MDN demonstrated limited benefits to rearing fish in early summer, fresh MDN derived from spawning salmon benefitted rearing juveniles from fall through winter and into the following spring (Figure 3.9). Taken collectively, these results suggest that watershed scale MDN effects linked to adult spawner abundance have the potential to affect stock productivity in Coho and Chinook salmon.

Juvenile salmon size and MDN assimilation: The association between MDN assimilation and fork length suggested that MDN played an important role in allowing fish to achieve greater size. Site MDN assimilation was positively linked to both individual and mean fork length in fall and winter and individual MDN assimilation demonstrated a consistent, positive relationship with fish length that was stronger in older fish and only absent in the youngest age classes (age-0 Coho and Chinook salmon in early summer). While the relationship between fork length and individual MDN assimilation likely indicates that larger fish simply assimilated more MDN, the positive relationship between site MDN and

fork length in the fall and winter suggests that increasing spawner abundance leads to larger juveniles. Size advantages derived from MDN use suggests substantial effects on survival given that larger fish are less prone to predation (Sogard 1997), less likely to suffer from disturbances such as flooding (Pearsons and others 1992; Bell and others 2001; Pess and others 2011), and are more competitive in defending territories (Ejike and Schreck 1980; Reinhardt 1999; Nielsen 1992; Rosenfeld and Hatfield 2006). Growth of juvenile salmon in freshwater environments is often limited as freshwater resources often fail to provide larger prey items necessary to sustain growth as metabolic needs escalate with increasing size (Beauchamp 2009). By providing large, energy rich prey items, marine subsidies may play a critical role in allowing fish to attain greater size than would be possible from freshwater resources alone (Armstrong and others 2010). Thus, the length ~ individual MDN relationship absent in age-0 fish in summer, but present in age-1+ fish, was evident in both age classes in fall, was strongest in winter and persisted in smolt (Figure 3.10). Fish size and associated gape width limit access to salmon eggs and fry, as well as large-bodied invertebrates associated with MDN such as caddisflies and blow fly larvae (Pearsons and Fritts 1999; Armstrong and others 2010), and thus once fish pass these size thresholds they experience the benefit of larger, richer prey items (Armstrong and others 2010).

While fish size was consistently related to individual MDN assimilation, there was often a neutral relationship to growth rates (R/D) that at first glance appears contradictory. However, R/D are relative measurements; a larger fish with the same R/D as a smaller fish is actually accumulating more mass. Thus the individual MDN relationship to size (positive) and growth (neutral) may be indicative of how marine subsidies allow larger fish to *maintain* growth as freshwater and terrestrial sources fail to meet energetic needs (Beauchamp 2009).

Early summer parr and residual MDN from past years' spawning: Prior to salmon spawning, residual MDN did not appear beneficial to age-0 Coho and Chinook salmon while age-1+ Coho Salmon demonstrated a mixed response to MDN. Residual MDN aided age-1+ Coho Salmon in achieving greater size but for age-1+ fish that remained in fresh water rather than migrate to sea as smolt, resources

associated with residual MDN were inferior relative to other resources available in early summer (Figures 3.2 and 3.9). Furthermore, early in the growing season fish allocate resources towards somatic growth at the expense of lipid accumulation (Metcalfe and others 2002) and it may be that such fish target residual MDN. As such, age-1+ Coho Salmon assimilating residual MDN had relatively low condition prior to the arrival of salmon spawners.

These results may also stem from the physiological "decision", based on threshold size and body condition (Stefansson and others 2008), on whether to undergo smoltification and migrate to the ocean *or* remain in fresh water for another year as parr. In the fall prior to smolting, salmon may either begin the process of smoltification by maximizing somatic growth at the expense of lipid accumulation or forego smoltification and enter a period of anorexia at the onset of winter (Stefansson and others 2008). Pre-smolts become more concentrated in late fall due to increased schooling and reduced territorial behavior associated with smoltification (Stefansson and others 2008) and limited over-wintering habitat (Cunjak 1996; Cunjak and others 1998). Additionally, Coho Salmon are more abundant where there are more adult Pink Salmon (Nelson and Reynolds 2014) which subsequently translates to greater MDN assimilation (Joy and others *in prep*[a]), with resultant enhancement of growth, size, and body condition (Figure 3.8). The following summer age-1+ fish remaining in fresh water are either parr that "decided" to forego smoltification in the fall *or* pre-smolt that, due to poor body condition, reverted to parr in the spring (Stefansson and others 2008). Pre-smolt that maintained adequate body condition migrate from the watershed as smolt leaving behind those that failed to maintain adequate condition even though they were past the size threshold necessary for initial smoltification. Similarly, parr that "decided" against smolting in the fall may also have benefitted from MDN through increased size but suffered worse condition as they emerged from winter anorexia. Thus, it may indeed be likely that poor summer condition in MDN enriched sites reflects the losers of density-dependent competition (non-smolt remaining in early summer) after the winners (smolt) migrated to sea. While speculative in nature, these results indicate possibly

intriguing and important interplay between smolt production, over winter performance, and MDN dynamics.

Fall and winter parr performance metrics and annual pulses of marine subsidies: After adult Pink, Chum, and Chinook salmon had spawned, juvenile salmon demonstrated a strong positive response to MDN in the fall and late winter (Figure 3.9). Fall MDN assimilation was a function of Pink and Chinook salmon escapements and indicative of the annual pulse of marine subsidies (Joy and others *in prep*[a]). Fall MDN was positively related to juvenile salmon length and condition and was also associated with higher growth rates in off-channel habitat for Coho Salmon (Figure 3.9). Given that energy deficiency is a main cause of winter mortality (Cunjak 1996; Cunjak and others 1998), the positive association between fish size, condition, and MDN assimilation suggests that larger escapements of Pink and Chinook salmon could increase over-winter survival in both juvenile species.

High water events and MDN. Our analysis suggested that the benefits of MDN to juvenile Coho Salmon in the fall may have been related to water levels as high water events pushed MDN into off-channel habitats where it positively affected juvenile salmon. While risking spurious conclusions with only three years of data, we believe the high contrast in water levels during this study coupled with anecdotal observations merit some discussion of these dynamics. During moderate and stable water levels salmon carcasses and associated scavengers accumulated on beaches while the directional flow of water from ponds into the river proper limited the transport of MDN into off-channel habitat. During high-water events river water flowed back into off-channel habitat, transforming ponds and connecting channels into sloughs. Flooding and high water mobilized MDN by sweeping carcasses and scavenging invertebrates (such as blow fly larvae, family Calliphoridae) into the river and even scoured salmon redds as evidenced by the presence of fertilized salmon eggs in salmon diets, even in off-channel habitat (personal observation). During this high water period, MDN assimilation in "ponds" rose to that of sloughs and channels (Joy and others *in prep*[a]) through this reversal of resource flow, and juvenile growth rates and size were positively linked to MDN. High water thus appeared to increase the value of marginally

connected water bodies by amplifying the amount of habitat available, redistributing nutrients (including MDN) and mobilizing MDN deposited on banks. Although the short data series limits our interpretation, these results suggest the need for future investigations of how water levels, habitat, and MDN interact to affect productivity. Indeed, while our research suggests the benefits of flooding events to Coho Salmon, recent research suggests that high flow may have detrimental effects on Chinook Salmon (Neuswanger and others 2015).

Smolt and MDN assimilation: MDN use by outmigrating smolt was beneficial to Chinook Salmon in the form of growth rates and fish size, suggesting possible effects on marine survival as Chinook Salmon transition to the marine environment. These results suggest substantial benefits from MDN to overall stock productivity given that size-selective mortality on smolt during early entry to the marine environment is thought to be a critical component in determining adult returns (Beamish and others 2004; Duffy and Beauchamp 2011).

Coho Salmon smolts did not appear to benefit from MDN as clearly as did Chinook Salmon, perhaps because Coho Salmon were more susceptible to density-dependent effects within the drainage during the years of this study. While Coho Salmon smolt demonstrated a positive relationship between individual MDN assimilation and both size and condition, site MDN assimilation was overall negatively related to fish size and condition (Figure 3.7). Although sample size may offer a partial explanation for this discrepancy given only two rivers and three years of data, the difference may also stem from the relative abundance of each species. Chinook Salmon spawner abundance was very low during the years of this study and below escapement (spawner abundance) goals set by the Alaska Department of Fish and Game (Menard and others 2013). Coho Salmon, in contrast, are very abundant in the drainage and exploitation on this species is relatively low (Mennard and others 2013; Joy and others *in prep*[b]). It is thus reasonable to surmise that juvenile Coho Salmon could be more susceptible to density-dependent effects that may exceed environmental and MDN effects. In contrast, less abundant juvenile Chinook Salmon are free

from density-dependent effects and thus year to year variation in performance may be more responsive to environmental effects such as MDN.

Smolt abundance: Qualitative examination of Coho Salmon smolt abundance estimates suggests that MDN may have affected smolt abundance through effects on over-winter survival. Over-winter survival is partially a function of fish size and condition (Quinn and Peterson 1996; Zabel and Achord 2004), both of which were positively associated with MDN in fall and over-wintering fish (Figure 3.9). The over-wintering period is often considered a survival bottleneck that may limit freshwater productivity and factors affecting over-winter survival may consequently have a profound impact on spring smolt abundance (Cunjak 1996; Cunjak and others 1998). High smolt MDN assimilation may be partially a product of high winter MDN assimilation (Joy and others *in prep*[a]) and thus, high fall and winter MDN may lead to higher survival rates *and* higher smolt MDN assimilation, subsequently producing a correlation between smolt MDN assimilation and smolt abundance as seen in the North River (Figure 3.8.C).

While smolt abundance did not vary similarly to spawner biomass in the previous year (Figure 3.8.A), the variability in the age structure of the smolt population suggests that declining adult spawner abundance meant fish required more time to achieve the size and condition to smolt. This subsequently led to more age-2+ smolts and fewer age-1 smolts. The age at which Coho Salmon parr undergo smoltification is flexible and dependent on fish size and condition (Quinn 2005). Our results demonstrated that fewer spawners lead to lower growth rates, smaller size and worse condition in rearing parr. Consequently, at lower spawner abundance, Coho Salmon took longer to attain the size and condition necessary to smolt and hence the proportion of age-2+ Coho Salmon smolt in both populations was relatively high, even as other factors determined overall abundance in the mainstem Unalakleet River (Figure 3.8.A).

These inferences are of course limited by the short term nature of the data, but do make sense in light of the relationships we documented between MDN assimilation and juvenile salmon performance metrics. Given that MDN assimilation is a function both of salmon escapements and retention from prior years

(Joy and others *in prep*[a]), it would likely take a long term data series with a broad range of escapements to observe a significant correlation between Coho Salmon smolt production and Pink Salmon escapements similar to that documented in Washington State rivers (Zimmerman 2011). Pink Salmon escapements were modest and declining during this study, ranging from 46,668 to 147,674 at the North River counting tower compared to 2.5 and 6.5 million between 2004 and 2006 (Menard and others 2013) and thus the range of escapements in our study may not have been sufficient to demonstrate strong relationships between Coho Salmon smolt abundance and Pink Salmon escapements. Nevertheless, our results suggest potential effects on over-winter survival and age-at-smolting that could produce correlations between Pink Salmon escapements and Coho Salmon productivity in a longer term data set.

Management implications: This study aimed to bridge the gap between salmon escapements and juvenile salmon performance by scaling up findings from smaller scale MDN studies to the watershed level and ultimately assess the potential for MDN from all spawning salmon to influence Coho and Chinook salmon productivity. Coho Salmon productivity is largely a function of freshwater habitat quality and quantity (Bradford and others 1997, 2000) and these results demonstrate how spawner abundance and resultant MDN partially defines habitat quality as it relates to juvenile salmon. Environmental and biological effects need to be relatively large to be informative to fisheries management (Adkison 2009), and effect sizes and MDNR^2 values were modest in our study, thus suggesting debate over whether MDN effects were strong enough to influence productivity. However, despite modest effect sizes, there were numerous positive trends that taken collectively suggest a significant effect of Pink Salmon escapements on rearing Coho Salmon, particularly in light of modest spawner abundance during the years of this study (Menard and others 2013). Furthermore, on a population level, Coho and Pink salmon in Norton Sound (including the North River) demonstrate similar trends in abundance over time and these correlative relationships are best explained by an influence of Pink Salmon on Coho Salmon via marine nutrients (Joy and others *in prep*[b]). Results from this project demonstrated mechanisms that would produce such correlations (Figure 3.9, Joy et al *in prep*[a]). In conjunction with two decades of experimental studies

(Wipfli and others 1998, 1999, 2003; Bilby and others 2003; Heintz and others 2004, 2010; Scheurell and others 2007; Denton and others 2009; Armstrong and others 2010; Rinella and others 2012) and long term smolt data series in other systems (Zimmerman 2011; Shaul and others 2014), our study provides compelling evidence that Coho Salmon productivity is at least partially a function of Pink Salmon escapements where these species overlap in time and space.

Given the evidence, it would be prudent to explore the incorporation of Pink Salmon spawner abundance into management plans for Coho Salmon in Norton Sound and other regions where these species coexist. Initial efforts should focus on forecasting adult returns to determine if modified spawner-recruit models can be a useful predictive tool. Multi-species management models could then be developed that incorporate Pink Salmon spawner abundance into Coho Salmon spawner-recruit models with maximum sustained yields (MSY) calculated for both species. These models should be compared to single-species spawner-recruit models to determine how escapement (spawner abundance) goals would change from those currently established by management agencies. Ultimately, a cost benefit analysis would be useful to determine economic gains and losses if forecasting was improved and multispecies models suggest curtailing Pink Salmon harvests to promote Coho Salmon returns.

Chinook Salmon also demonstrated a strong benefit from MDN derived from spawning Pink and Chinook salmon that was on par with the benefits to Coho Salmon, suggesting that Chinook Salmon productivity may also be partially dependent on marine subsidies. Given prolonged declines in Alaska Chinook Salmon populations in the past two decades (Orsi and others 2013), further research into the effects of MDN on Chinook Salmon is certainly warranted. MDN use by juvenile Coho and Chinook salmon was associated with Chinook as well as Pink salmon spawning abundance in the Unalakleet River (Joy and others *in prep*[a]). Given that Chinook Salmon often undertake long spawning migrations to inland waterways (Brown and others 2017), these results beg further research into MDN dynamics associated with Chinook Salmon populations in more inland locations. In addition to examining MDN dynamics in Chinook Salmon populations, researchers should also examine spawner-recruit relationships in Chinook

Salmon that incorporate MDN benefits from adult spawners. With regard to interspecific interaction between Chinook and other salmon species, it is unclear whether Chinook Salmon would demonstrate the kind of population level relationships seen in Coho and Pink salmon (Michael 1995; Shaul and others 2014; Joy and others *in prep*[b]) given that Chinook Salmon spend a much greater proportion of their life cycle in the marine environment (66 – 88%). However, our results certainly justify an examination of long-term Chinook Salmon brood tables to determine if such effects are present. Furthermore, understanding how increased escapements of Pink and Chinook salmon increases growth of rearing Chinook Salmon and how that may ultimately impact survival and condition at smolting may ultimately provide managers with alternative avenues for addressing Chinook Salmon productivity.

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LITERATURE CITED

Adams, L. G., S. D. Farley, C. A. Stricker, D. J. Demma, G. H. Roffler, D. C. Miller and R. O. Rye. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? Ecological Applications 20: 251-262.

Adkison, M. A. 2009. Drawbacks of complex models in frequentist and Bayesian approaches to natural-resource management. Ecological Applications 19: 198-205.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91: 1445-1454.

Arnason, A. N., C. W. Kirby, C. J. Schwarz, and J. R. Irvine. 1996. Computer analysis of data from stratified mark-recovery experiments for estimation of salmon escapements and other populations. Canadian Technical Report of Fisheries and Aquatic Science 2106: vi+37 p.

Barton, K. 2016. Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package = MuMIn.

Beamish, R. J., C. Mahnken and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. Transactions of the American Fisheries Science 133: 26-33.

Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. American Fisheries Society Symposium 70: 1-19.

Bell, E., W. G. Duffy and T. D. Roelofs. 2001. Fidelity and survival of juvenile Coho Salmon in response to a flood. Transactions of the American Fisheries Science 130: 450-458.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bernard, D. R., and R. A Clark. 2009. Importance of marine-derived nutrients in establishing escapement goals for Pacific salmon. American Fisheries Society Symposium 71: 147-164.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Science 53: 164-173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Science Sci. 55:1909-1918.

Bilby, R. E., E. W. Beach, B. R. Fransen, J. K. Walter, and P. A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of the American Fisheries Society 132: 733-745.

Biro, P. A., A. E. Morton, J. R. Post and E. A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Science 61: 1513-1519.

Bolger, T. and P. L. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. Journal of Fish Biology 34: 171-182.

Booth, G. D., M. J. Niccolucci, and E. G. Schuster.1994. Identifying proxy sets in multiple linear regressions: an aid to better coefficient interpretation. –US Dept. of Agriculture, Forest Service.

Bradford, M. J., R. A. Myers, and J. R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production Canadian Journal of Fisheries and Aquatic Science 57: 677-686.

Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society 126: 49-64.

Brakensiak, K. E., and D. G. Hankin. 2007. Estimating overwinter survival of juvenile Coho Salmon in a northern California stream: accounting for effects of passive interated transponder tagging mortality and size-dependent survival. Transactions of the American Fisheries Society 136: 1423-1437.

Brown, R. J., R. J. Henszey, A. von Finster, and J. H. Eiler. 2017. Catalog of Chinook Salmon spawning areas in the Yukon River basin in Canada and the United States. Journal of Fisheries and Wildlife Management 8: 558-587.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Calderone, E. M., M. Wagner, J. St. Onge-Burns, and L. J. Buckley. 2001. Protocol and guide for estimating nucleic acids in larval fish using a fluorescence microplate reader. Northeast Fisheries Science Center Reference Document 01-11; 22p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.

Calcagno, V. and C. de Mazancourt. 2010. Glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1-29.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59: 197-242.

Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. Canadian Journal of Fisheries and Aquatic Science 59: 1257-1265.

Conover, W. J. 1980. Practical nonparametric statistics 2nd ed. John Wiley & Sons, New York. 428. pp

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Science 53(Suppl. 1): 267-282

Cunjak., R. A., T. D. Prowse and D. L. Parrish. 1998. Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent"? Canadian Journal of Fisheries and Aquatic Science 55(Suppl. 1): 161-180.

Darroch, J. N. 1961. The two sample capture-recapture census when tagging and sampling are stratified. Biometrika 48: 241-260.

Denton, K. P., H. B. Rich Jr., and T. P. Quinn. 2009. Diet, movement, and growth of Dolly Varden in response to Sockeye Salmon subsidies. Transactions of the American Fisheries Society 138: 1207-1219.

Dietrich, J. P. and R. A. Cunjak. 2006. Evaluation of the impacts of Carlin tags, fin clips, and Panjet Tattoos on juvenile Atlantic salmon. North American Journal of Fisheries Management 26: 163-169.

Dormann, C. F., J. Elith, S/ Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell and S. Lautenbach. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 35: 001-020.

Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Science 68: 232-240.

Ebersole, J. L., P. J. Wigington Jr., J. P. Baker, M. A. Cairns, M. R. Robbins Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton and S. G. Leibowitz. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. Transactions of the American Fisheries Society 135: 1681-1697.

Ejike, C. and C. B. Schreck. 1980. Stress and Social Hierarchy Rank in Coho Salmon. Transactions of the American Fisheries Society 109: 423-426.

Finstad, A. G., O. Ugedal, T. Forseth and T. F. Næsje. 2004. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Science 61: 2358-2368.

Galipaud, M., M. A. F. Gillingham, M. David and F-X. Dechaume-Moncharmont. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods in Ecology and Evolution 5: 983-991.

Hanisch, J. R., W. T. Tonn, C. A. Paszkowski and G. J. Scrimgeour. 2010. $\delta^{13}C$ and $\delta^{15}N$ signatures in muscle and fin tissues: nonlethal sampling methods for stable isotope analysis of salmonids. North American Journal of Fisheries Management 30: 1-11.

Hanson, K. C., K. G. Ostrand, A. L. Gannam, and S. L. Ostrand. 2010. Comparison and validation of nonlethal techniques for estimating condition in juvenile salmonids. Transactions of the American Fisheries Society 139: 1733-1741.

Hargreaves, N. B. and R. J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Canadian Journal of Fisheries and Aquatic Science 42: 659-668.

Heintz, R. A., B. D. Nelson, J. Hudson, M. Larson, and L. Holland. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Transactions of the American Fisheries Society 133: 559-567.

Heintz, R. A., M. S. Wipfli, and J. P. Hudson. 2010. Identification of marine-derived lipids in juvenile coho salmon and aquatic insects through fatty acid analysis. Transactions of the American Fisheries Society 139: 840-854.

Herbinger, C. M., and G. W. Friars. 1991. Correlation between condition factor and total lipid content in Atlantic salmon, *Salmon salar* L., parr. Aquaculture Research 22: 527-529.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 47: 2181-2194.

Joy, P. J., C. S. Stricker, W. Jones, M. Tyers, A. C. Seitz, and M. S. Wipfli. *In prep*[a]. Bridging the gap between salmon spawner abundance and marine nutrient use by juvenile: seasonal cycles and landscape effects at the watershed scale.

Joy, P. J., M. D. Atkison, A. C. Seitz, and M. S. Wipfli. *In prep*[b]. Disentangling auocorrelation from marine-subsidy and ocean effects: do Pink Salmon escapements affect Coho Salmon productivity?

Lynch, S. M. 2007. Introduction to Applied Bayesian Statistics and Estimation for Social Scientists. Springer-Verlag, New York.

MacLean, S. A., E. M. Caldarone and J. M. St. Onge-Burns. 2008. Estimating recent growth rates of Atlantic salmon smolts using RNA-DNA ratios from nonlethally sampled tissues. Transactions of the American Fisheries Society 137: 1279-1284.

Madsen, H. and P. Thyregod (2011). Introduction to General and Generalized Linear Models. Chapman & Hall/CRC. ISBN 978-1-4200-9155-7.

Manly, B. F. J. 1997 RT: a program for randomization testing. Western EcoSystems Technology Inc, Cheyenne, WY.

Menard, J., J. Soong, S. Kent, and A. Brown. 2013. 2012 Annual management report Norton Sound – Port Clarence Area, and Arctic-Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 13-28, Anchorage.

Metcalfe, N. B., C. D. Bull and M. Mangel. 2002. Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. Evolutionary Ecology Research 4: 871-881.

Michael Jr., J. H. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. Northwest Science, 69: 228-233.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters, 11(5), 470-480.Mosher, K. H. 1969. Identification of Pacific salmon and steelhead trout by scale characteristics. United States Department of the Interior, U. S. Fish and Wildlife Service, Bureau of Commerical Fisheries, Washington, D. C., Circular 317.

Nelson, M. C. and J. D. Reynolds. 2014. Time-delayed subsidies: interspecies population effects in salmon. PLoS ONE 9(6): e98951.

Neuswanger, J. R., M. S. Wipfli, M. J. Evenson, N. F. Hughes, and A. E. Rosenberger. 2015. Low productivity of Chinook salmon strongly correlates with high summer stream discharge in two Alaskan rivers in the Yukon drainage. Canadian Journal of Fisheries and Aquatic Sciences 72:1125–1137.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121: 617-634.

Orsi, J. A., M. V. Sturdevant, E. A. Fergusson, W. R. Heard, and E. V. Farley Jr. 2013. Chinook Salmon marine migration and production mechanisms in Alaska. North Pacific Anadromous Fish Commission Technical Report No. 9: 240-243.

Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board Canada 28: 1503-1510.

Pearsons, T. N. and A. L. Fritts. 1999. Maximum size of chinook salmon consumed by juvenile coho salmon. North American Journal of Fisheries Management 19: 165-170.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemlages. Transaction of the American Fisheries Society 121: 427-436.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson and T. P. Quinn. 2011. The influence of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. Transaction of the American Fisheries Society 140: 883-897.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Linking Alaskan salmon fisheries management with ecosystem-based escapement goals: a review and prospectus. Fisheries 34: 124-134.

Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20-22, Vienna, Austria.

Post, J. R. and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology, 82(4); 1040-1051.

Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. American Fisheries Society in association with University of Washington Press. Seattle, WA.

Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Science 53: 1555-1564.

R Core Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reinhardt., U. G. 1999. Predation risk breaks size-dependent dominance in juvenile coho salmon (*Oncorhynchus kisutch*) and provides growth opportunities for risk-prone individuals. Canadian Journal of Fisheries and Aquatic Society 56: 1206-1212.

Rinchard, J. S. Czesny and K. Dabrowski. 2007. Influence of lipid class and fatty acid deficiency on survival, growth, and fatty acid composition in rainbow trout juveniles. Aquaculture 264: 363-371

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz and M. J. Rinella. 2012. Pacific salmon (Oncorhynchus spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Society 69: 73-84.

Rosenfeld, J. S and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Society 63: 683-698.

Ruggerone, G. T. and D. E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: implications for salmon management. North American Journal of Fisheries Management 12: 87-102.

Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. Ashley Steel, and W. L. Reichert. 2009. Nonlethal sampling of fish caudal fins yields valuable stable isotope data for threatened and endangered fishes. Transactions of the American Fisheries Society 138: 1166-1177.

Scarnecchia, D. L. 1979. Variation of scale characteristics of coho salmon with sampling location on the body. Progressive Fish Culturist 41(3):132-135.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, second edition. Charles Griffen and Company, Limited, London.

Shaul, L. D., K. F. Crabtree, K. C. Koolmo, K. M. Koolmo, J. V. Nichols, and H. J. Geiger. 2014. Studies of coho salmon and other Oncorhynchus species at Ford Arm Creek, 1982 – 2009. Alaska Department of Fish and Game, Fishery Manuscript Series No. 14-02, Anchorage.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.

Stefansson, S. O., B. Th. Björnsson, L. OE. Ebbesson, and S. D. McCormick. 2008. Smoltification. In: Finn, R. N., B. G. Kapoor (Eds.), Fish Larval Physiology. Science Publishers, Enfield, pp. 639-681.

Stock, B. C. and B. X. Semmens. 2013. MixSIAR GUI User Manual, version 1.0. http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR

Stroup, W. W. 2012. Generalized linear mixed models: modern concepts, methods and applications. Chapman & Hall/ CRC Press, Boca Raton, FL.

Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129: 527-538.

Wang, S. Y., J. L. Lum, M. G. Carls, and S. D. Rice. 1993. Relationship between growth and total nucleic acids in juvenile Pink Salmon, *Oncorhynchus gorbuscha*, fed crude oil contaminated food. Canadian Journal of Fisheries and Aquatic Society 50: 996-1001.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Society 55: 1503-1511.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132: 371-381.

Wipfli, M. S., J. Hudson, D. T. Chaloner and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Society 56: 1600-1611.

Wipfli, M. S., J. P. Hudson, J. P. Caouette and N. L. Mitchell. 2010. Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic lveles in streamside experimental channels. Transactions of the American Fisheries Society 139: 824-839.

Zabel, R. W. and S. Achord. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. Ecology, 85; 795-806.

Zimmerman, M. 2011. 2011 wild coho forecasts for Puget Sound, Washington Coast, and Lower Columbia. Washington Department of Fish and Wildlife, Olympia, Washington.

TABLE LEGENDS

Table 3.1. Abundance estimates of Coho Salmon smolt migrating from the Unalakleet and North Rivers in 2011 – 2013 produced using temporally stratified Darroch estimates (Darroch 1961). Where size stratification was required, the abundance estimate for each size strata is presented as is the number of temporal periods for each sampling event as determined by diagnostic tests (Appendix C) and program SPAS (Arnason and others 1996).

Table 3.1. Abundance estimates of Coho Salmon smolt migrating from the Unalakleet and North Rivers in 2011 – 2013.

River	Year	Size Category (mm)	# Marked	# Examined in 2nd Event	# Marked Fish in 2nd Event	Capture Prob.	SE Cap. Prob.	1st event temporal periods	2nd event temporal periods	Estimate	SE	Low 95% CI	High 95% CI
Unalakleet	2011	80–88	1,110	1,186	18	0.0162	0.0038	1	3	73,203	16,983	39,915	106,490
		89–97	1,781	5,167	97	0.0115	0.0046	2	5	135,445	40,012	57,022	213,867
		> 97	1,058	7,152	51	0.0482	0.0066	1	3	148,369	20,196	108,784	187,954
		All								**357,017**	**47,930**	**263,075**	**450,959**
	2012	80–85	1,187	187	5	0.0042	0.0019	1	2	44,394	19,545	6,086	82,702
		86–91	2,668	1,699	37	0.0048	0.0049	3	3	215,719	85,355	48,423	383,015
		> 91	9,750	5,730	182	0.0181	0.0020	2	5	311,141	25,603	260,959	361,323
		All								**571,254**	**91,230**	**392,442**	**750,066**
	2013	80–85	3,712	749	37	0.0029	0.0023	2	4	90,174	29,727	31,909	148,438
		86–94	7,155	2,383	99	0.0102	0.0020	2	4	165,219	16,299	133,272	197,166
		> 94	7,933	3,331	100	0.0155	0.0046	2	3	272,112	29,248	214,785	329,438
		All								**527,505**	**44,775**	**439,746**	**615,264**
North	2011	**All**	1,372	1,880	27	0.0144	0.0027	2	1	**95,532**	**18,072**	**60,110**	**130,953**
	2012	80–89	920	114	13	0.0241	0.0090	3	4	11,837	5,413	1,228	22,447
		90–97	1,335	247	45	0.0453	0.0147	2	5	10,175	1,595	7,049	13,301
		> 97	2,691	780	86	0.0394	0.0180	3	6	28,070	3,766	20,688	35,452
		All								**50,082**	**6,784**	**36,785**	**63,379**
	2013	**All**	8,214	1,453	180	0.1662	0.0234	5	2	**89,379**	**19,918**	**50,339**	**128,420**

FIGURE LEGENDS

Figure 3.1. Digital elevation model (DEM) of the Unalakleet River drainage, the location of the Unalakleet River weir and North River counting tower used for monitoring salmon escapements in the watershed, and the location of sampling sites (hexagons, numbered for reference) in the Unalakleet River drainage. Out-migrating smolts were sampled near the counting tower and below the Unalakleet River weir.

Figure 3.2. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile Coho Salmon in the Unalakleet River watershed in summer as predicted from model-averaged mixed effect generalized linear models. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

Figure 3.3. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the fork length and Ricker's condition factor, *K*, of juvenile Chinook Salmon in the Unalakleet River watershed in fall as predicted by model-averaged mixed effect generalized linear models. Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

Figure 3.4. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile age-0 and age-1+ Coho Salmon in the Unalakleet River watershed in fall as predicted from model-averaged mixed effect generalized linear models. Where MDN effects were important ($I > 0.80$) the

effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

Figure 3.5. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the fork length, and Ricker's condition factor, *K,* of juvenile Coho Salmon in the Unalakleet River watershed in winter as predicted by model-averaged mixed effect generalized linear models. Effects are depicted in channel (red line) and slough (green short dashed line) habitats. The lower two plots demonstrate interactions of individual and site MDN assimilation on *K* (left plot, $I = 0.25$) and the interaction of fork length and individual MDN assimilation on *K* (right plot, $I = 0.56$, interaction in top ranked model). Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

Figure 3.6. Plots depicting the interaction of marine derived nutrients (MDN) and water depth on Coho Salmon fall fork length ($I = 0.65$ and variable in top ranked model) and fall R/D in different habitats (Depth*Habitat $I = 0.27$; Depth*Site MDN $I = 0.47$) as predicted from model averaged mixed effect generalized linear models. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

Figure 3.7. Plots depicting the predicted relationship between site and individual marine-derived nutrient assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K,* of juvenile Coho and Chinook salmon smolts as predicted by model averaged mixed effect generalized linear models. Where MDN effects were important ($I > 0.80$) the effects are depicted for smolt emigrating from the mainstem Unalakleet (gold line) and North (purple long dashed line) rivers. Plots present importance scores (*I*) of

the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variable, year.

Figure 3.8. Relationships between Coho Salmon smolt abundance, spawner biomass from the prior year and smolt marine-derived nutrient (MDN) assimilation (proportion of tissue derived from MDN) in the Unalakleet and North rivers. A) The relationship between smolt abundance (black diamonds and solid black line), age-1 smolt abundance (white squares and dashed line) and age-2+ smolt abundance (grey triangles and grey lines line). Error bars represent standard errors. B) The relationship between smolt MDN assimilation for North (grey circles and triangles) and Unalakleet (black circles and triangles) river smolt in comparison to total spawner biomass (circles and dashed lines) and Pink Salmon biomass (triangles and solid lines) estimates from the year prior to smolting. Error bars represent 95% credibility intervals (Joy and others *in prep*[a]). C) Relationship between smolt MDN assimilation and smolt abundance (Table 1). Horizontal and vertical error bars represent 95% credibility and confidence intervals, respectively.

Figure 3.9. A conceptual model of how marine-derived nutrients impacts rearing Coho Salmon during the freshwater portion of their life cycle. Height of bars represents the amount of variation in the data explained by MDN and associated interactions (MDNR^2 value; see text for explanation) for variables where importance, I, was greater than 80% for either site or individual marine-derived nutrient assimilation.

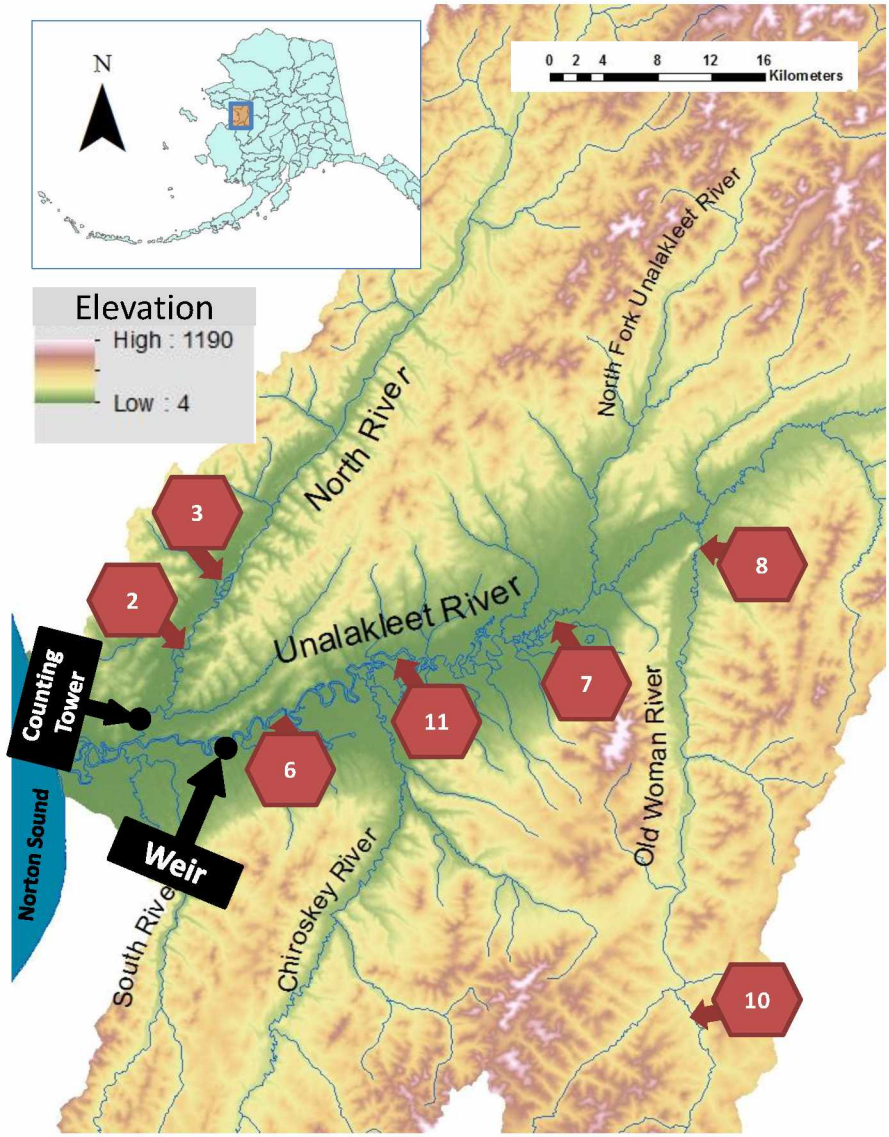


Figure 3.1. Digital elevation model (DEM) of the Unalakleet River drainage, the location of the Unalakleet River weir and North River counting tower used for monitoring salmon escapements in the watershed, and the location of sampling sites (hexagons, numbered for reference) in the Unalakleet River drainage. Out-migrating smolts were sampled near the counting tower and below the Unalakleet River weir.

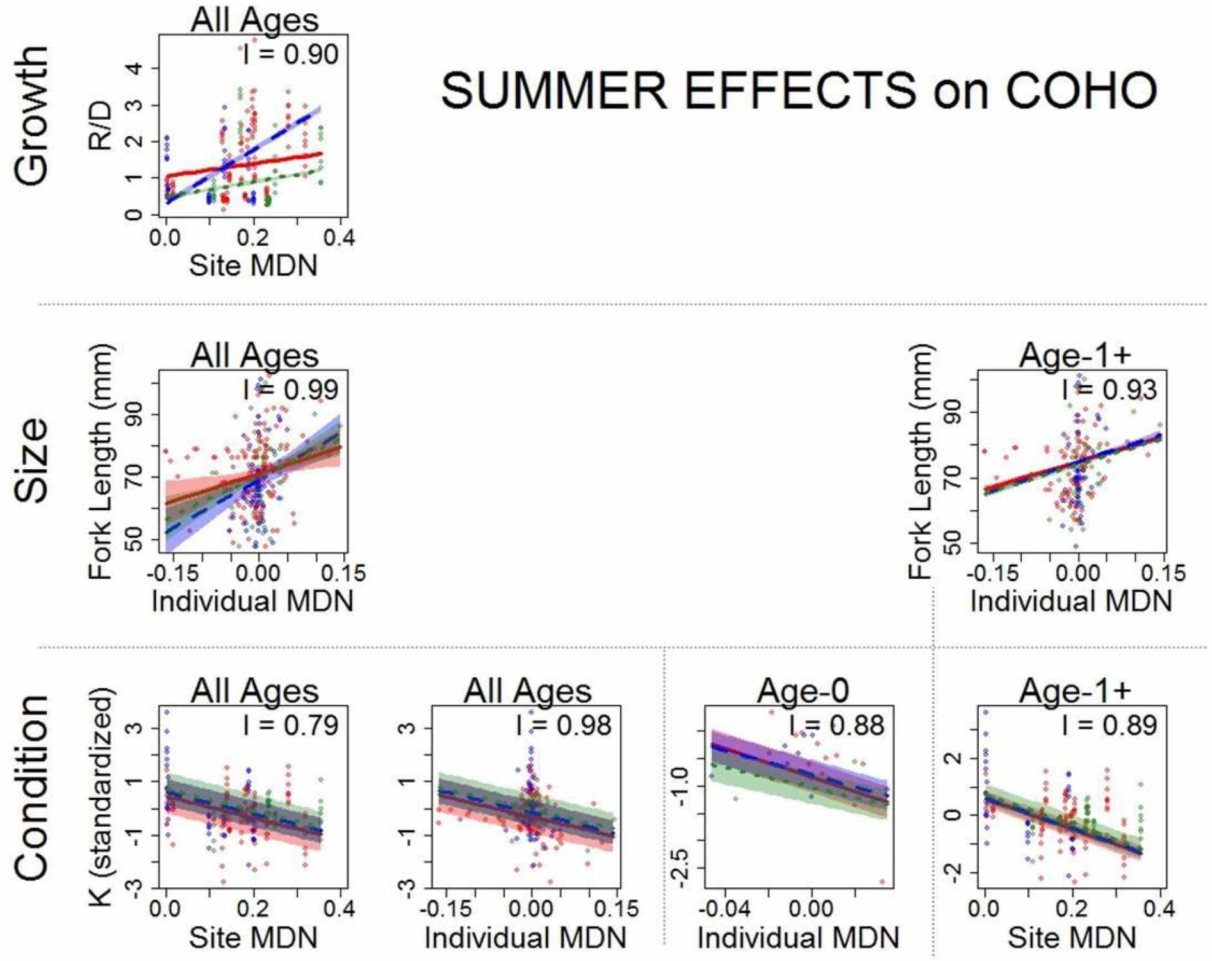


Figure 3.2. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile Coho Salmon in the Unalakleet River watershed in summer as predicted from model-averaged mixed effect generalized linear models. Colors denote channel (red), slough (green) and pond (blue) habitat.

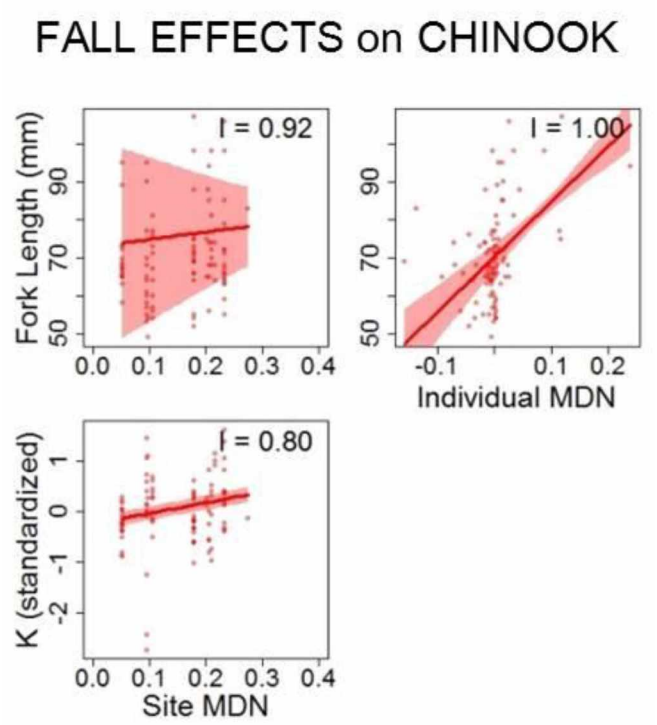
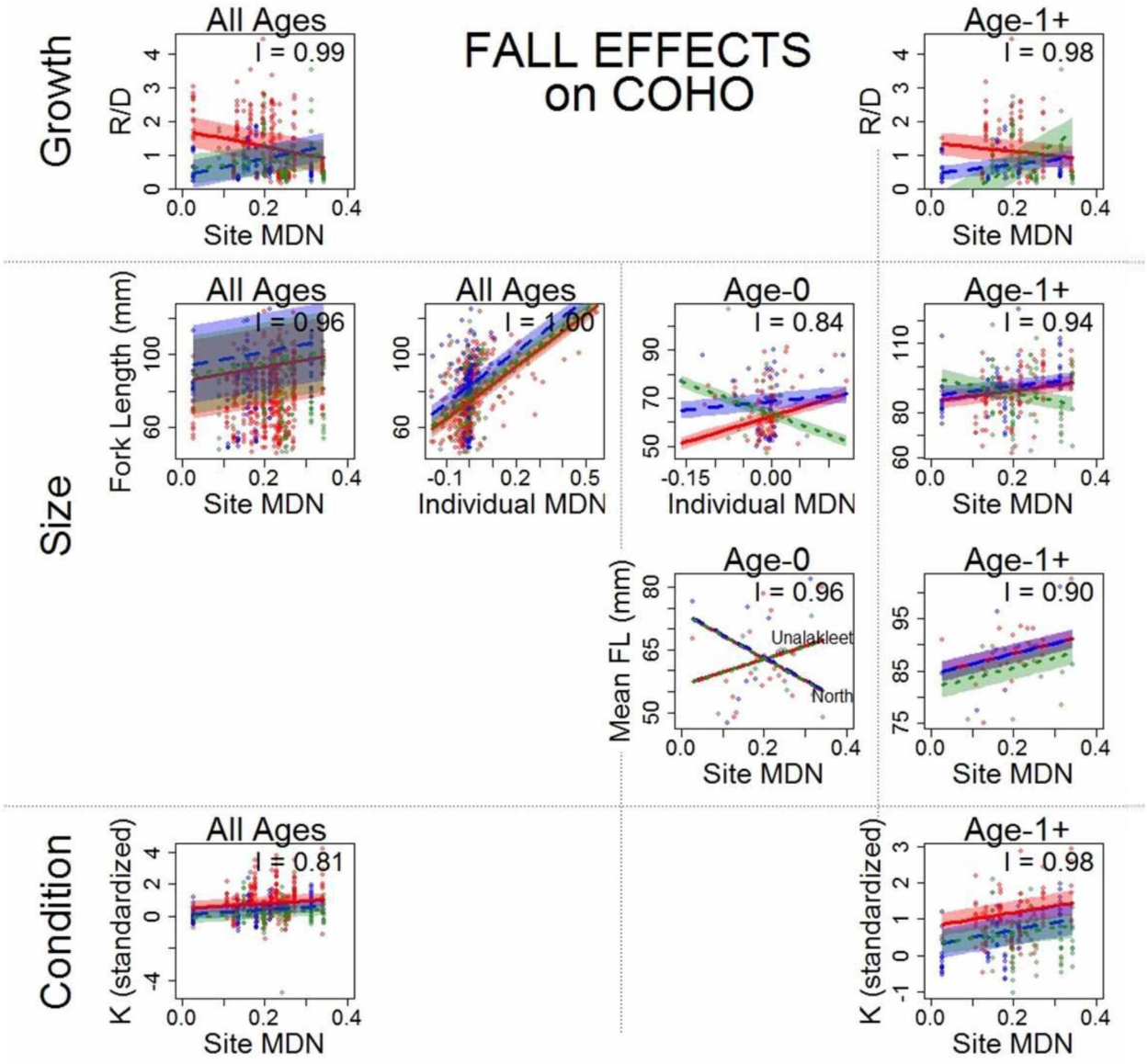


Figure 3.3. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the fork length and Ricker's condition factor, *K*, of juvenile Chinook Salmon in the Unalakleet River watershed in fall as predicted by model-averaged mixed effect generalized linear models.



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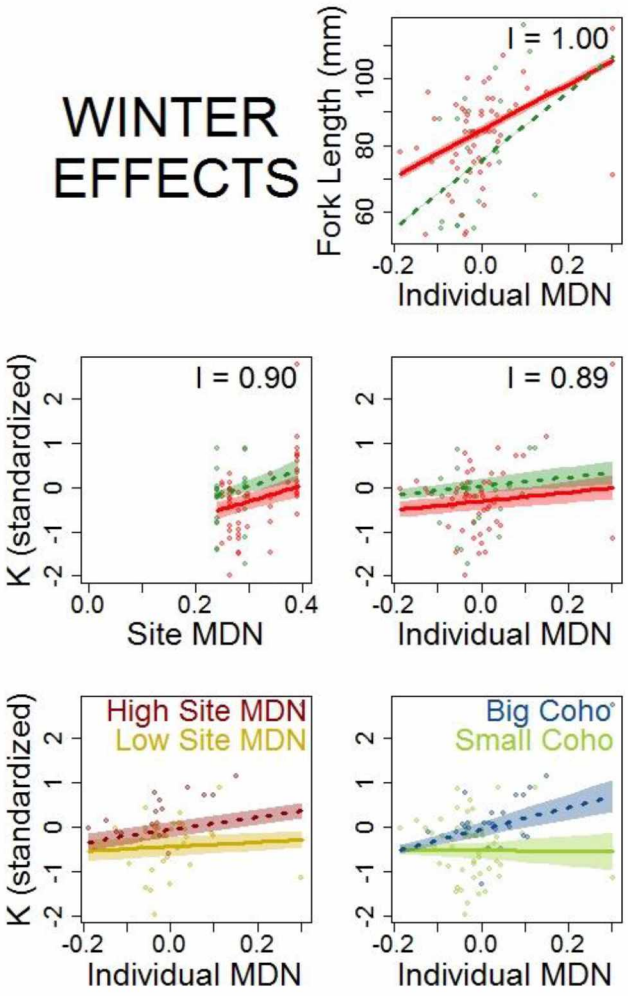
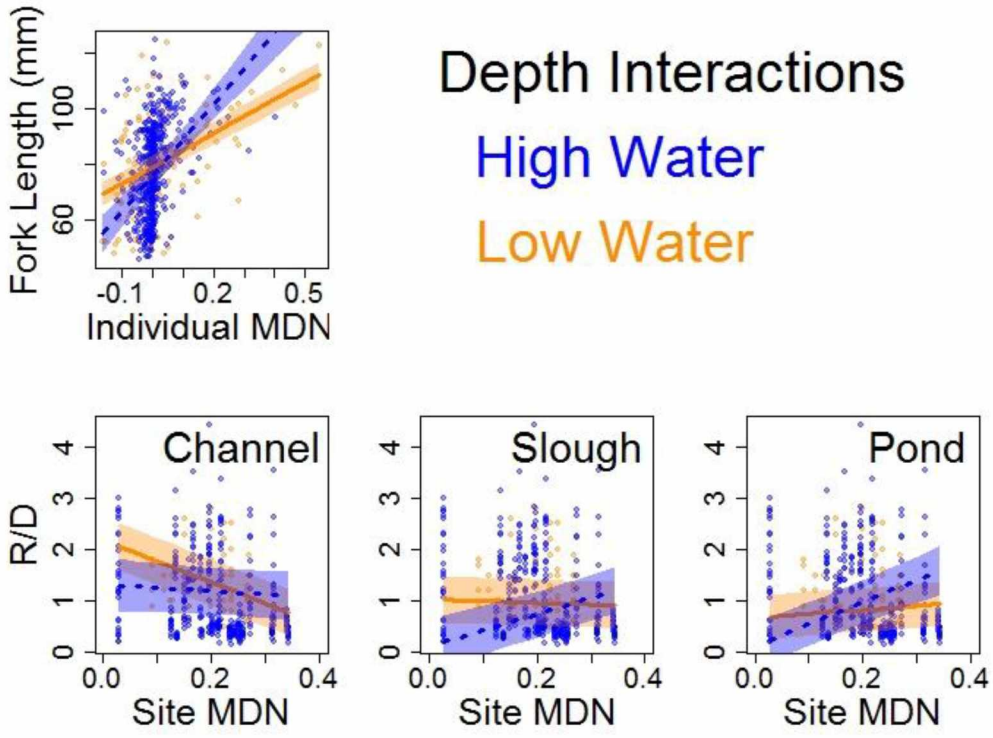


Figure 3.5. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the fork length, and Ricker's condition factor, *K*, of juvenile Coho Salmon in the Unalakleet River watershed in winter as predicted by model-averaged mixed effect generalized linear models. Colors in the top three plots denote channel (red) and slough (green) habitat.



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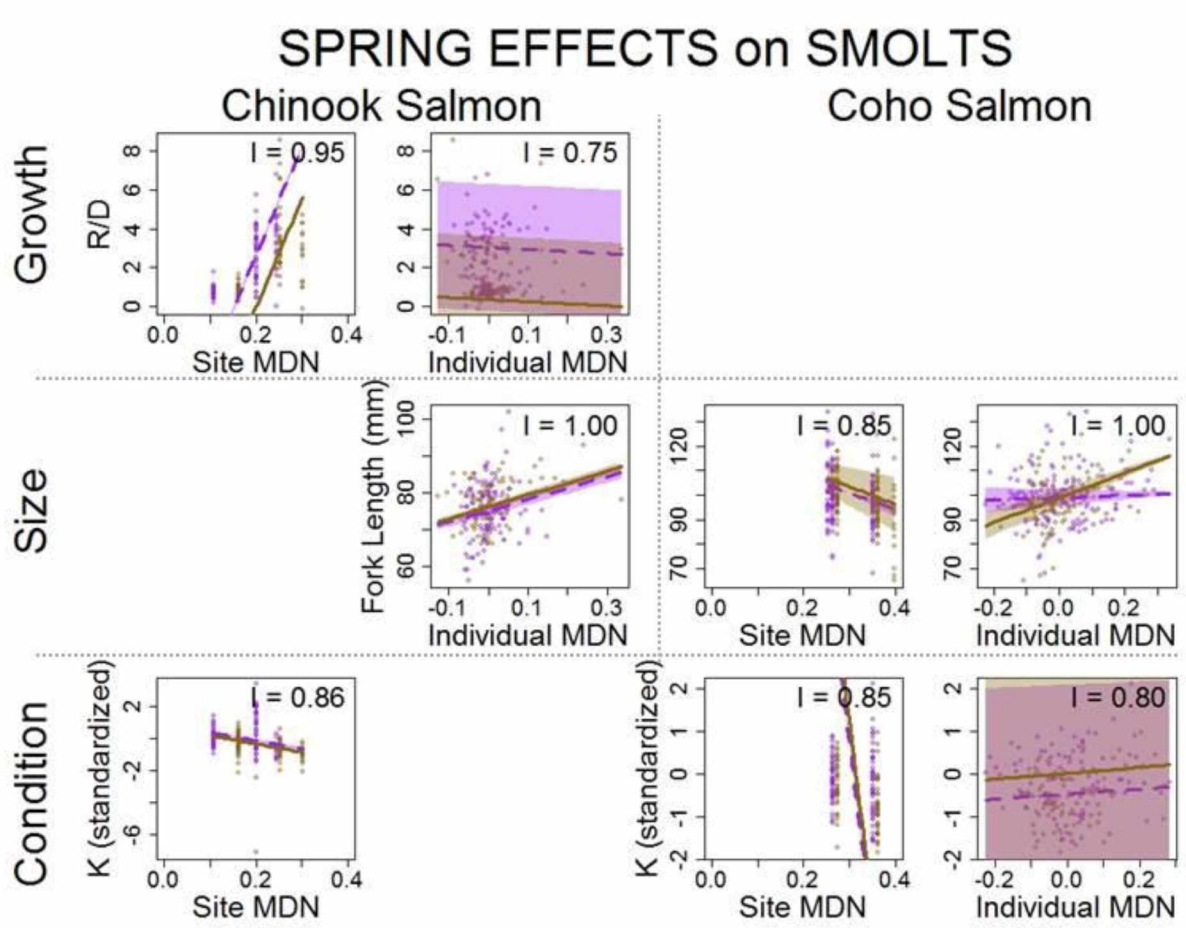


Figure 3.7. Plots depicting the predicted relationship between site and individual marine-derived nutrient assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile Coho and Chinook salmon smolts as predicted by model averaged mixed effect generalized linear models. Colors denote the mainstem Unalakleet River (purple) and the North River (gold).

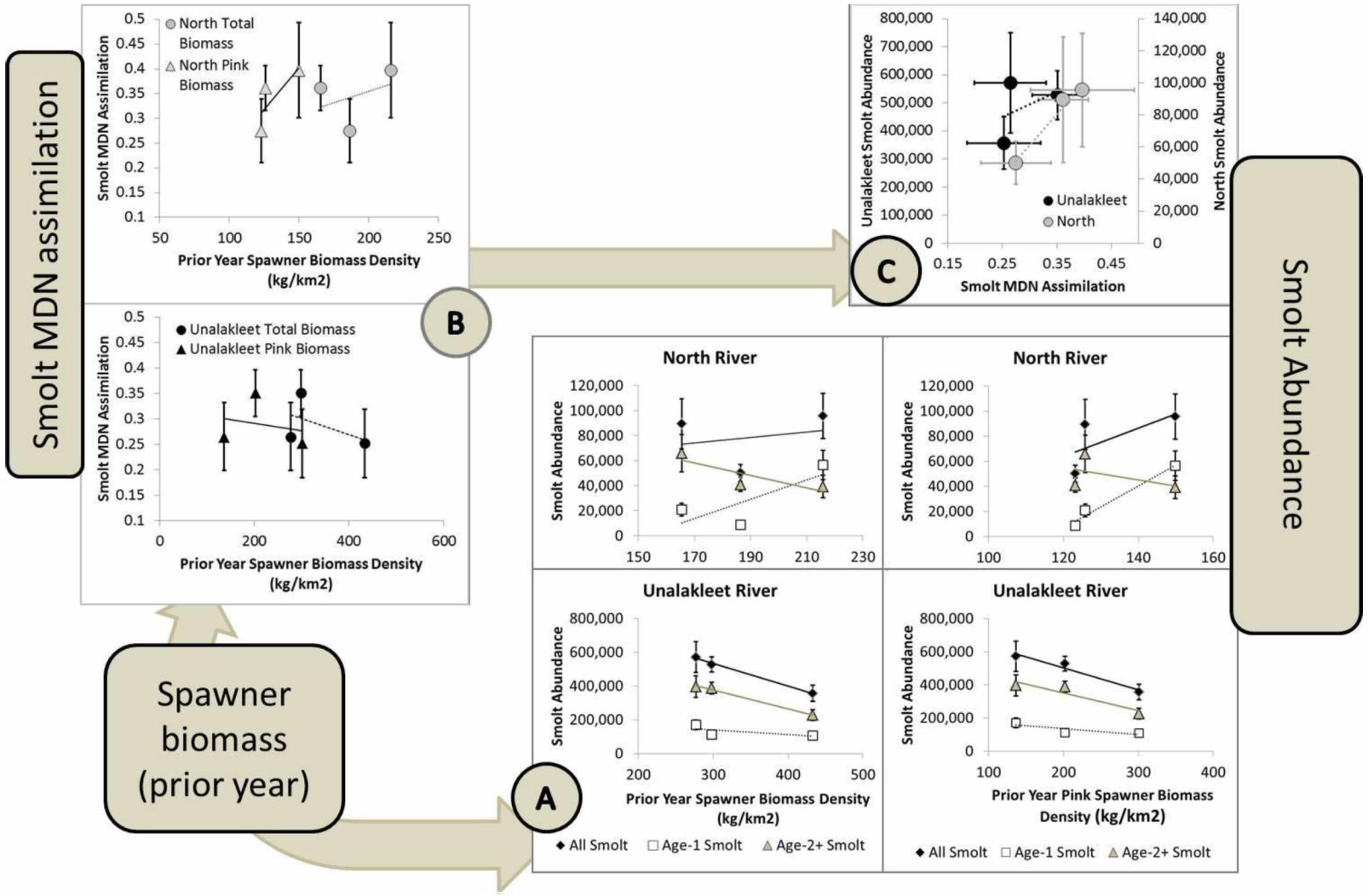


Figure 3.8. Relationships between Coho Salmon smolt abundance, spawner biomass from the prior year and smolt marine-derived nutrient (MDN) assimilation (proportion of tissue derived from MDN) in the Unalakleet and North rivers.

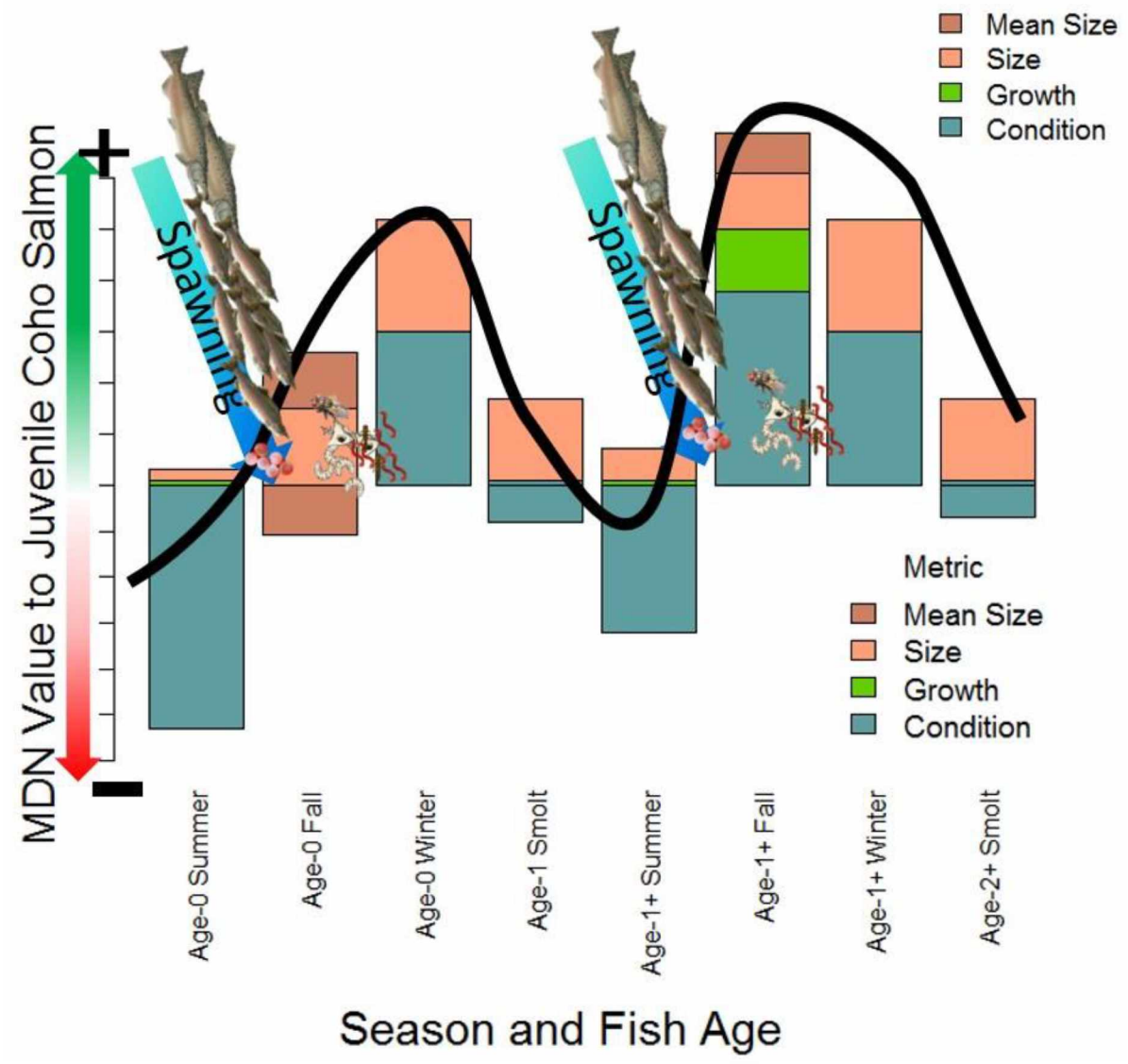


Figure 3.9. A conceptual model of how marine-derived nutrients impacts rearing Coho Salmon during the freshwater portion of their life cycle. Height of bars represents the amount of variation in the data explained by MDN and associated interactions (MDNR^2 value; see text for explanation) for variables where importance, *I*, was greater than 80% for either site or individual marine-derived nutrient assimilation.

Appendix 3.A. Examination of the mark-recapture assumptions necessary to produce unbiased estimates in a closed mark-recapture experiment on emigrating smolt and diagnostic tests to examine equal probability of capture.

For smolt abundance estimates to be unbiased using mark-recapture methodology (Seber 1982), certain assumptions must be met: 1) the population was closed to births, deaths, emigration and immigration, 2) marking and handling did not affect catchability, 3) fish did not lose their marks between marking and recapture, and 4) fish demonstrated equal probability of capture during either the first or second event (Seber 1982). The assumption that the population was closed was not likely violated, given that Coho Salmon did not migrate prior to ice-out (evident from small catches and parr-like coloration of fish immediately after ice-out). Although there is no way to test assumption 2, we sought to curtail handling effects by minimizing holding and handling times and by not releasing obviously stressed or injured fish. Furthermore, handling mortality was examined three times during the study and fish held overnight experienced negligible mortality (< 1%). Double marking with dye and either a colored tattoo or fin notch assured that fish did not lose their marks between sampling events (assumption 3). Assumption 4, regarding equal probability of capture, was explicitly tested to determine appropriate stratification of data by fish length, capture gear, and temporal period. We examined size biases using Kolmogorov-Smirnov two sample tests (KS test, Conover 1980) using randomization methods (Manly 1997) and used contingency table analyses recommended by Seber (1982) to detect heterogeneity in capture probabilities by time and capture gear (Appendix A).

Unbiased abundance estimates also require that capture probabilities be equal for all smolt in either the first or second event or there be complete mixing of marked and unmarked fish between sampling events (Seber 1982). To determine how capture probabilities varied by fish length, Kolmogorov-Smirnov two sample tests (KS test, Conover 1980) were employed using randomization methods (Manly 1997) that allowed for the weighing of each observation based on the number of fish measured and the total number of fish captured each day. The two samples consisted of fish captured in minnow traps and fish captured

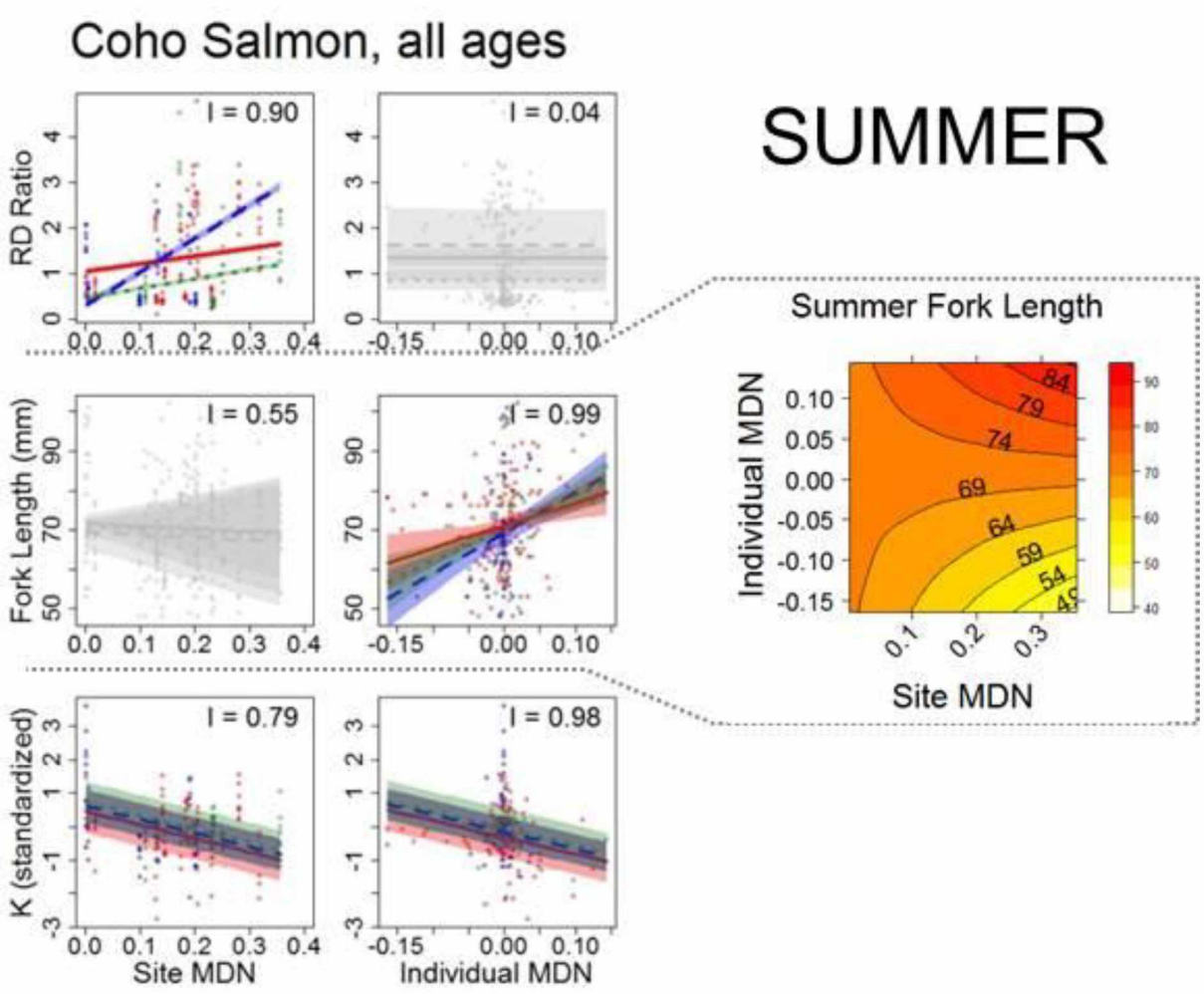
in either the screw or fyke trap. Each measured fish was given an unadjusted weight equal to the number of fish sampled divided by the total number of fish caught in the sample. Unadjusted weights (UAW) were adjusted such that

$$Adjusted\ Weight = {}^{UAW * Total\ \#\ measured}/_{\sum UAW} \quad (5)$$

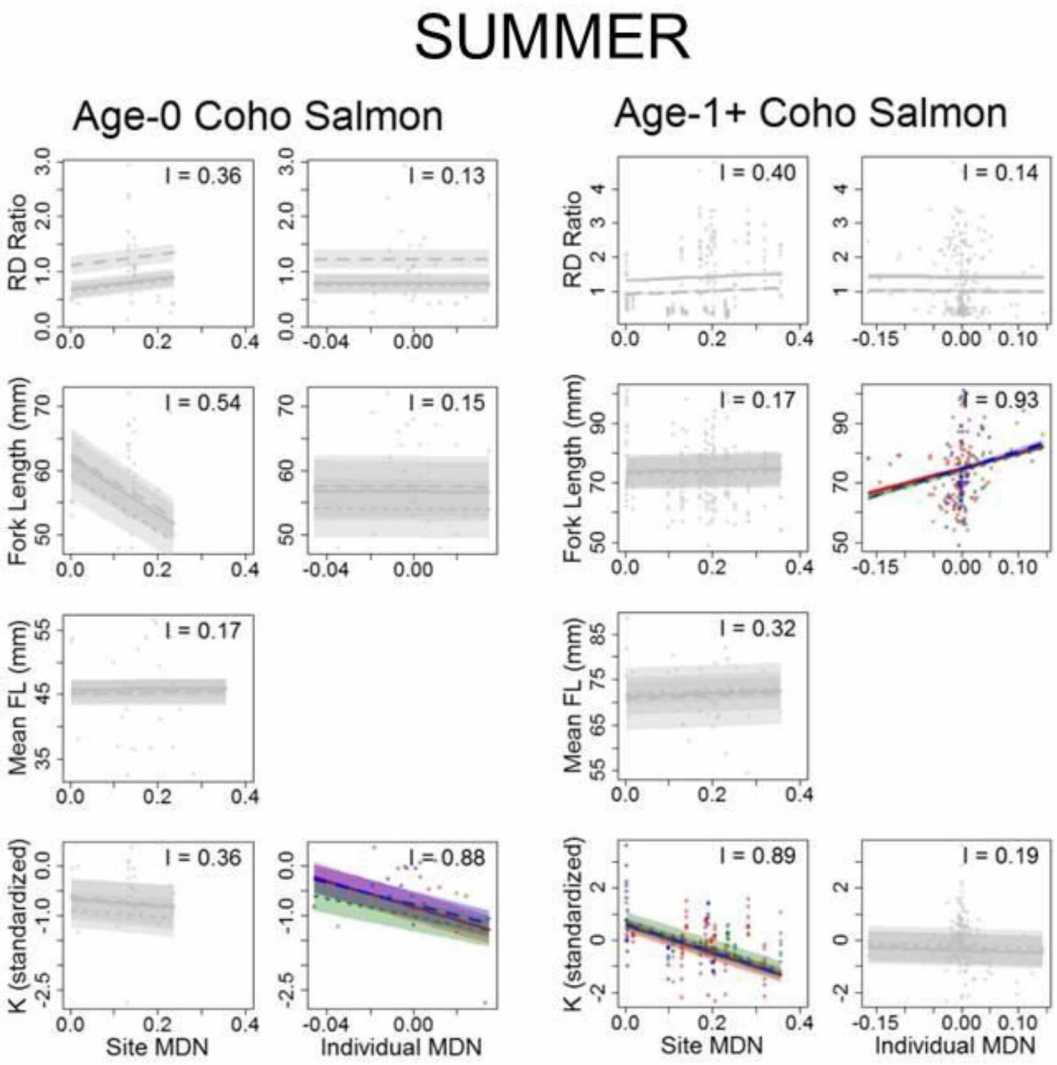
Cumulative distribution functions (CDFs) were constructed for each sample utilizing the adjusted weights. The KS statistic (Conover 1980) was calculated from the CDF of fish caught in minnow traps and fixed traps (screw trap or fyke trap). The randomization procedure used 10,000 iterations where 5% of the fish lengths were removed from each sample (minnow trap or fixed trap) and placed in the alternate sample. After each pass, a KS test was performed and the KS statistic recorded. Significance of the test was determined using the proportion of randomized KS tests that were greater than or equal to the original KS test (Manly 1997). If a significant result was produced ($\alpha = 0.05$) the data was stratified around the length at which the original CDFs were furthest apart. The procedure was repeated for each of the new size strata to determine if capture probabilities varied within each strata and until it failed to detect significant differences in capture probabilities within size strata.

Contingency table analyses recommended by Seber (1982) were used to detect heterogeneity in capture probabilities by time and capture gear. Heterogeneity in capture probabilities based on capture gear was examined utilizing chi-square tests (Seber 1982; Joy and Reed 2007). If capture probabilities were not significantly different in at least one event then data was not stratified by capture gear. If capture probabilities differed by gear in both events abundance estimates were stratified by gear as well as by time and size.

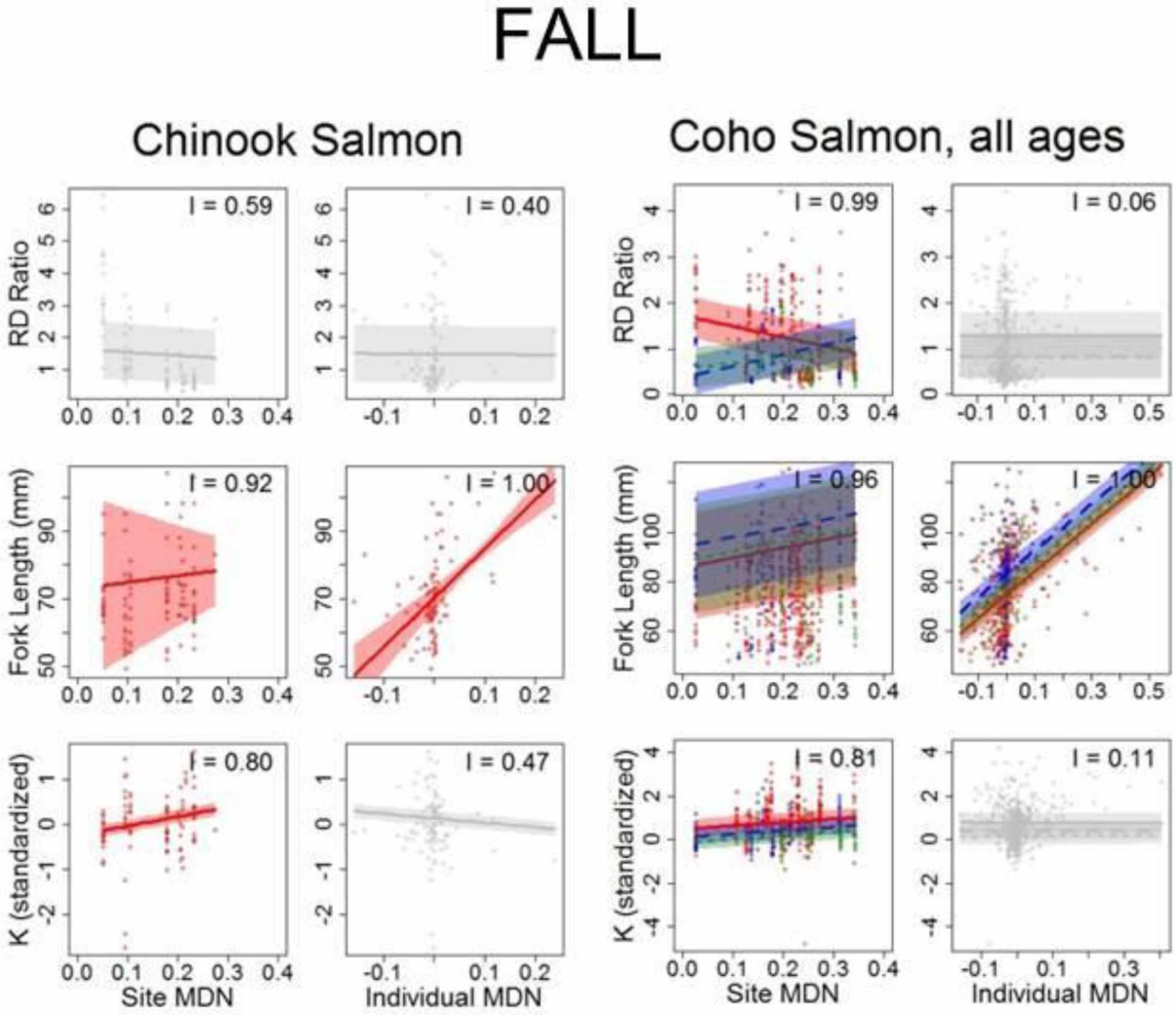
Temporal heterogeneity in capture probabilities was anticipated given the duration and variable conditions of the smolt migration. To determine temporal breaks and how to pool three day sampling periods, contingency table analysis was performed (Seber 1982; Joy and Reed 2007).



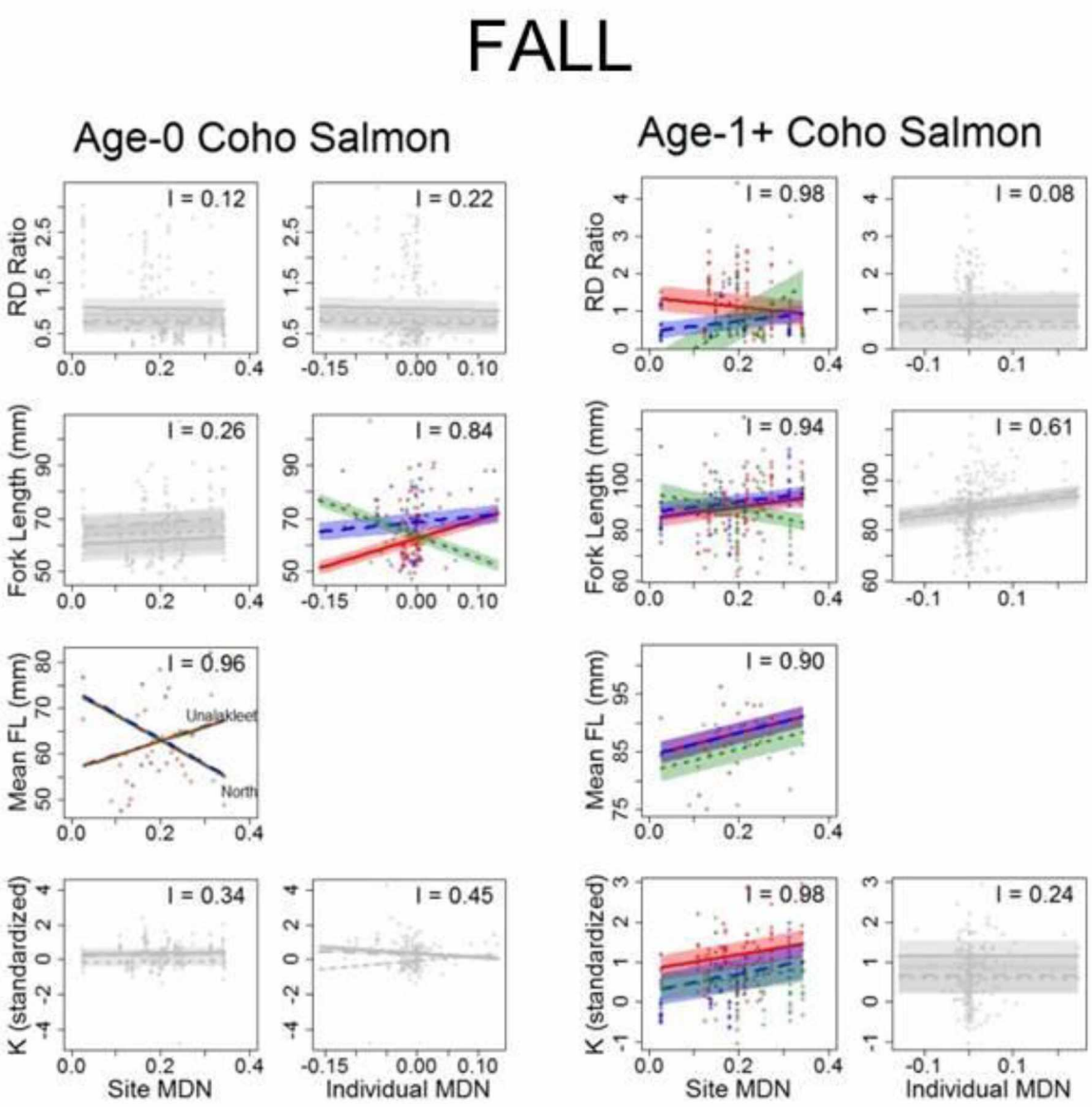
Appendix 3.B.1. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile Coho Salmon in the Unalakleet River watershed in summer as predicted from model-averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Contour plot illustrates the interaction of individual and site MDN on fork length of Coho Salmon. Plots present importance scores (I) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.



Appendix 3.B.2. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile age-0 and age-1+ Coho Salmon in the Unalakleet River watershed in summer as predicted from model-averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Plots present importance scores (I) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

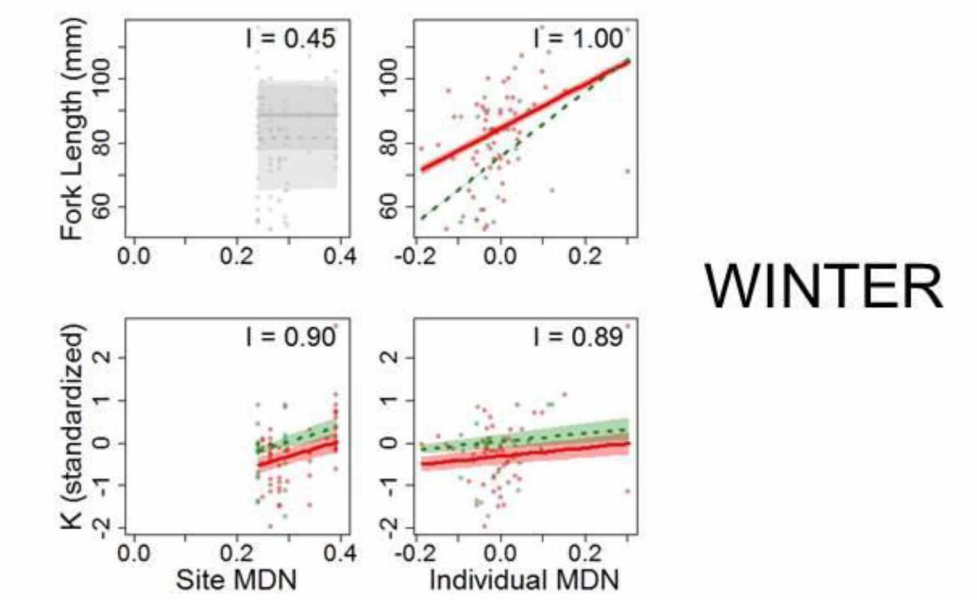


Appendix 3.B.3. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K,* of juvenile Coho and Chinook salmon in the Unalakleet River watershed in fall as predicted by model-averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Plots present importance scores (I) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.

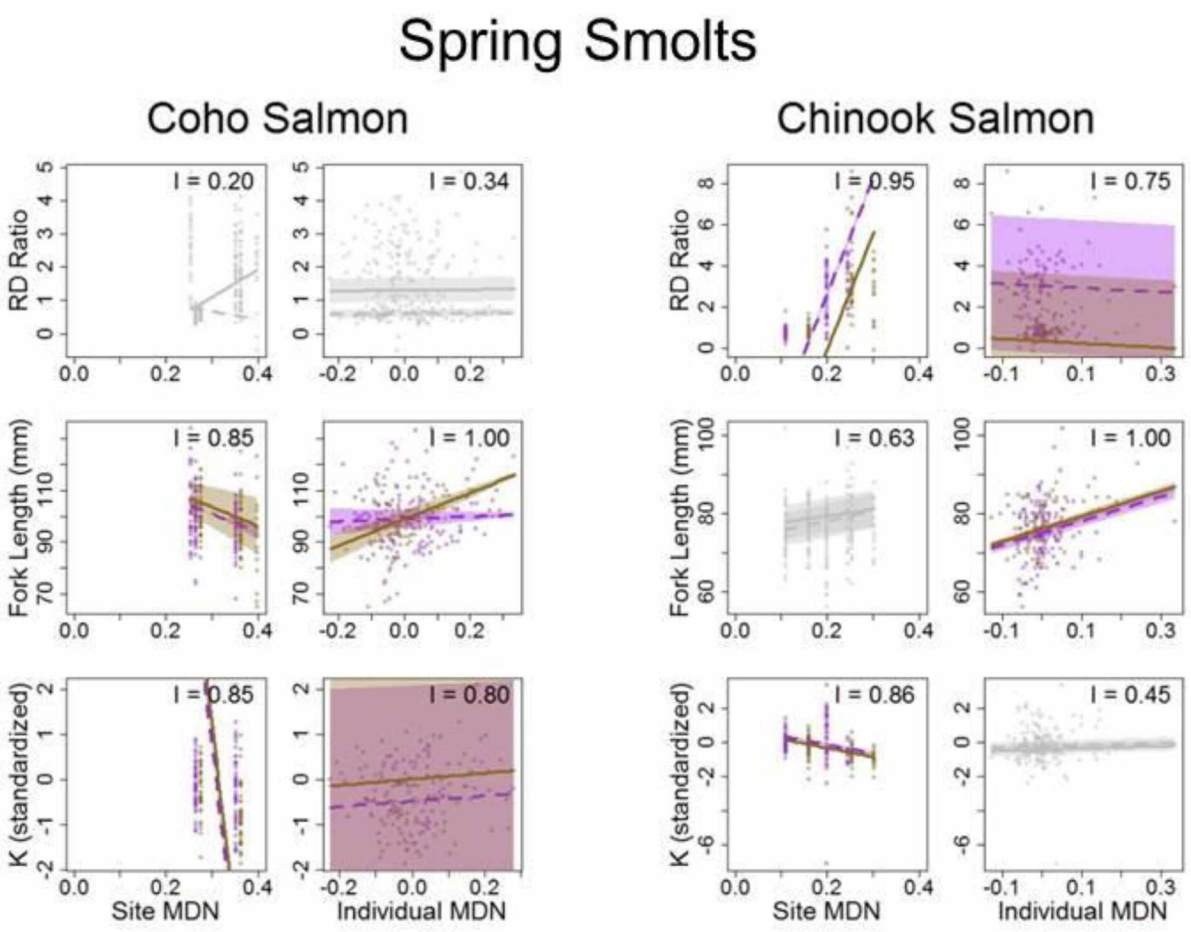


Appendix 3.B.4. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile age-0 and age-1+ Coho Salmon in the Unalakleet River watershed in fall as predicted from model-averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line), slough (green short dashed line) and pond (blue long dashed line) habitats (other colors represent overlapping confidence intervals). Plots present importance scores (I) of the site

and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.



Appendix 3.B.5. Plots depicting the predicted relationship between site and individual marine-derived nutrient (MDN) assimilation and the fork length, and Ricker's condition factor, *K,* of juvenile Coho Salmon in the Unalakleet River watershed in winter as predicted by model-averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted in channel (red line) and slough (green short dashed line) habitats. Contour plots demonstrate interactions of individual and site MDN assimilation on *K* (left contour plot) and the interaction of fork length and individual MDN assimilation on *K* (right contour) . Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variables, sampling site and year.



Appendix 3.B.6. Plots depicting the predicted relationship between site and individual marine-derived nutrient assimilation and the RNA:DNA ratio, fork length, and Ricker's condition factor, *K*, of juvenile Coho and Chinook salmon smolts as predicted by model averaged mixed effect generalized linear models. Where MDN effects were not important ($I < 0.80$) plots are depicted in grey scale. Where MDN effects were important ($I > 0.80$) the effects are depicted for smolt emigrating from the mainstem Unalakleet (gold line) and North (purple long dashed line) rivers. Plots present importance scores (*I*) of the site and individual MDN variables. Error polygons (shaded regions) represent one standard deviation of the average predicted values derived from the random variable, year.

Appendix 3.C.1. Results of diagnostic test for determining size biased heterogeneity in capture probabilities between first and second event sampling for Coho Salmon utilizing KS tests (see text). NFS denotes no further stratification required.

Year	River	Size Category	D statistic	P-value	Stratification Length
2011	Unalakleet	All	0.32	<0.01	88 mm
		> 88 mm	0.21	0.02	97.5 mm
		≤ 88 mm	0.13	0.12	NFS
		> 88 & ≤ 97 mm	0.11	1.00	NFS
		> 97 mm	0.08	0.13	NFS
	North	All	0.12	0.80	NFS
2012	Unalakleet	All	0.19	<0.01	91.6 mm
		≤ 91 mm	0.23	<0.01	87.5 mm
		≤ 87 mm	0.21	0.02	85.5 mm
		≤ 85 mm	0.03	0.99	NFS
		Although diagnostic tests indicated a size category between 85 and 87 mm, stratification was made around 86 mm to avoid small sample sizes			
		≥ 86 & ≤ 91 mm	0.11	0.39	NFS
		> 91 mm	0.07	0.13	NFS
	North	All	0.12	< 0.01	97.3 mm
		≤ 97 mm	0.11	0.10	89.5 mm
		> 89 & ≤ 97 mm	0.04	0.99	NFS
		≤ 89 mm	0.08	0.64	NFS
		> 97 mm	0.02	1.00	NFS
2013	Unalakleet	All	0.26	< 0.01	95.5 mm
		≥ 95 mm	0.05	0.71	NFS
		< 95 mm	0.15	0.03	85.5 mm
		> 85 & < 95 mm	0.06	0.89	NFS
		≤ 85 mm	0.05	0.97	NFS
	North	All	0.09	1	NFS

Appendix 3.C.2. Significance results (P-values) of diagnostic tests for determining bias in capture probabilities in first event sampling for Coho Salmon based on capture gear utilizing χ^2 tests (see text).

Year	River	Size Category	Fyke or Rotary Screw Trap	Minnow Traps	Gear Pooled
2011	Both	Only minnow traps were used for 1st event sampling			
2012	Unalakleet	All	< 0.01	< 0.01	0.01
		80-85 mm	0.01	0.26	0.95
		86-91 mm	< 0.01	0.03	0.83
		> 91 mm	< 0.01	0.20	< 0.01
	North	All	0.46	0.86	0.67
		80-89 mm	0.30	0.42	0.31
		90-97 mm	0.58	1.00	0.85
		> 97 mm	0.62	0.32	0.49
2013	Unalakleet	All	< 0.01	0.06	0.871
		80-85 mm	0.51	0.90	0.80
		86-94 mm	< 0.01	0.11	1.00
		> 94 mm	0.13	0.16	0.58
	North	All	0.02	< 0.01	< 0.01

CONCLUSIONS

This dissertation demonstrated that MDN derived from spawning Pink Salmon significantly affected Coho and Chinook salmon and the cumulative evidence presented here suggests measurable effects on stock productivity that may ultimately prove useful to fisheries managers. My examination of correlative patterns in Coho and Pink salmon population dynamics, while accounting for autocorrelation, consistently indicated that MDN from spawning Pink Salmon was likely affecting Coho Salmon productivity in Norton Sound and Southeast Alaska. This conclusion was evident on a finer scale in the Unalakleet River watershed where I examined the relationship between salmon escapements, juvenile salmon MDN assimilation, and juvenile salmon performance metrics such as size, growth and body condition. Assimilation of MDN by juvenile Coho and Chinook salmon in the Unalakleet River was a function of Pink and Chinook salmon escapements after summer spawning events and retention of MDN within the system was positively linked to habitat complexity. MDN assimilation was shown to increase size and improve body condition in juvenile salmon which would presumably increase survival rates (Quinn and Peterson 1996; Zabel and Achord 2004; Brakensiak and Hankin 2007; Pess et al. 2011). Although Coho Salmon smolt abundance was not directly related to escapement levels in my short term data series, the demonstrated effects on growth and condition suggested that declining escapements may have led to an older age distribution in the smolt population as slower growing fish required longer to achieve the size and condition to undergo smoltification.

Although this dissertation provides evidence on population level effects of MDN, actual estimates of juvenile salmon abundance and survival would provide more direct measures of productivity. Such relationships have seldom been documented but limited research by us and others highlights the promise of expanded research along these avenues. While Chapter 1 documented trends in adult abundance, I did not examine parr abundance and my evaluation of smolt abundance in Chapter 3 was limited by the short duration of the study. Furthermore, I did not directly measure survival rates, although I did examine factors such as growth, size, and body condition, that are very likely to affect juvenile salmon survival

rates both in freshwater (Quinn and Peterson 1996; Zabel and Achord 2004; Brakensiak and Hankin 2007; Pess et al. 2011) and during the first year at sea (Holtby et al. 1990; Beamish et al. 2004; Duffy and Beauchamp 2011). Direct estimates of juvenile abundance come from British Columbia where Coho Salmon parr abundance was positively related to spawning Pink Salmon abundance (Nelson and Reynolds 2014), and from Washington state where Coho Salmon smolt abundance was correlated with a function of Pink Salmon abundance (Zimmerman 2011). While my examination of Coho Salmon smolt abundance failed to detect any obvious correlation between smolt abundance and either smolt MDN levels or spawner biomass I did note a possible effect on the age distribution and age-at-smolting in Coho Salmon. Nevertheless, the short time series in my study likely limited my ability to discern complex relationships between spawner abundance, MDN, and smolt productivity. Indeed, obvious relationships between smolt abundance and MDN metrics were unlikely given that MDN content is a function of both salmon escapements and retention from prior years (Chapter 2) and Pink Salmon escapements in 2011 – 2013 were low and lacking in contrast relative to historical numbers (Menard et al. 2013). It would likely take a long term data series with a broad range of escapements to observe a significant correlation between Coho Salmon smolt and Pink Salmon escapements similar to that documented in Washington State rivers (Zimmerman et al. 2011).

Directly estimating survival and abundance in wild populations is an expensive and logistical challenge given the sample sizes required with large populations and low survival rates. If covariates of interest are expensive to obtain, which would be the case when measuring MDN content using stable isotope analysis, then costs can quickly become prohibitive. These projects are also most useful when conducted for an extended number of years so as to examine a broad range of environmental conditions. Coded-wire tagging (CWT) projects (Ohlberger et al. 2018) or passive-integrated transmitter (PIT) projects (Tattam et al. 2015) could provide the opportunity to measure both over-winter survival and early marine survival in addition to providing abundance estimates. Such projects would require large sample sizes, a means of sampling outmigrating smolt and substantive sampling of returning adults. A moderate sized watershed

such as the Unalakleet River could provide an ideal setting for such an investigation provided funding could be obtained. Producing smolt abundance estimates is a challenging and expensive proposition, but is the most direct means of measuring how MDN impacts freshwater productivity of salmon populations. Indeed, it is just this kind of data that demonstrated meaningful relationships between Pink Salmon abundance and Coho Salmon smolt productivity in Washington state (Zimmerman 2011).

Deciphering ecological effects in natural settings with short term data series is inherently difficult and a major shortcoming of this study was the brief duration of the Unalakleet River project. To address these shortcomings and truly evaluate productivity will ultimately require long term data series. Retrospective analysis using salmon scales (Howard et al. 2016), otolith chemistry (Walker and Sutton 2016), escapement data from management agencies (Munro 2018), and other sources are excellent approaches to address some of these questions. However, retrospective analyses can be challenging when the original study was not designed to address the questions of present day biologists. Establishing and funding long term projects is extremely challenging given federal and state funding cycles but should nevertheless be a priority for addressing important ecological questions. My study began to shed light on the association between escapements and MDN assimilation (Chapter 2) but a long term data series will ultimately be required to measure these relationships with the confidence required to modify and change existing management practices.

Further examination of escapement and harvest data from Alaska, Canada, and the Pacific Northwest would also provide valuable insights into interspecific and conspecific MDN interactions. While I examined Coho and Pink salmon escapement and harvest data in Chapter 1, many avenues of exploration remain given the large amount of MDN imported by other species, including Chum, Sockeye, and even Chinook salmon. Chum and Sockeye salmon provide large loads of nutrients to other systems, but due to their different life histories (including differing age structures in both fresh and salt water), correlations between these species and Coho Salmon would likely manifest differently from Pink-Coho salmon relationships. Biologists have examined how Sockeye Salmon are affected by MDN derived from

conspecifics (Schindler et al. 2005; Uchiyama et al. 2008; Adkison 2010) but there have been few studies examining how MDN from Sockeye Salmon benefits other economically important salmon species at the population level. Furthermore, juvenile stream-type Chinook Salmon (which rear for one year in freshwater) respond just as strongly to MDN as Coho Salmon while spawning adult Chinook Salmon migrate thousands of kilometers up rivers (Brown et al. 2017) and contribute MDN that is assimilated by juvenile salmon (Chapter 2).

Management implications

Despite remaining gaps in our understanding, current evidence justifies an exploration of ways to incorporate MDN into salmon management. Doing so will ultimately require further examination of escapement data and reconstructed brood tables to determine where MDN effects are occurring, which species deliver MDN, and which species benefit from them. Incorporating MDN relationships into management will require developing modified spawner-recruit models that consider MDN from other species as well as from conspecifics. Furthermore, examining smolt abundance data where they exist may provide more detailed insight into how spawner abundance affects smolt productivity.

Performing retrospective analysis of escapement and smolt abundance data can be difficult considering sometimes limited or flawed estimates. Many escapement monitoring projects only examine a portion of the species migrating into the watershed, making it problematic to examine interspecific relationships. In my examination of Pink and Coho salmon interactions, I found very few data series suitable for examination as Coho Salmon are incompletely counted due to late run timing and low exploitation, and Pink Salmon are often enumerated by highly inaccurate methods such as aerial and foot surveys. Encouraging management agencies to accurately count and cover all species migrating into a watershed throughout the duration of the runs should be a priority given that MDN (as well as other interspecific interactions) could be relevant and useful to management agencies. Furthermore, there are few long term smolt data series available that would provide a more precise evaluation of how MDN enhances

freshwater productivity. My results certainly make a compelling case for establishing long term smolt monitoring projects that allow straight forward measurements of freshwater productivity.

Despite limitations, further exploration of escapement data and associated brood tables should be the first step in adapting MDN based relationships into management practices. Identifying systems with significant MDN interactions will require constructing modified spawner-recruit models that incorporate escapements as an MDN metric. This may involve multi-species scenarios such as I examined in Chapter 1 where Pink Salmon escapements were a variable in Coho Salmon spawner recruit models. Such evaluations may include any number of salmon species where they overlap in time and space. Given how stream rearing salmonids such as Sockeye, Coho, and Chinook salmon benefit from densely spawning species including Sockeye, Pink, and Chum salmon. Furthermore, MDN effects may also involve conspecifics. For instance, Uchiyama et al. (2008) and Adkison (2010) explored conspecific MDN interactions in Sockeye Salmon populations and found that higher escapements may increase long-term harvests in some populations. My results demonstrated that Chinook Salmon both benefitted from MDN as rearing juveniles *and* provided MDN to systems as spawning adults. Developing spawner recruit models for Chinook Salmon that incorporate spawner abundance during the year following spawning by the parent generation (when spawners provide MDN for the rearing juveniles) should certainly be explored. Spawner recruit models that incorporate MDN based variables can then be compared to spawner-recruit models currently used in management to determine if they better explain variability in recruitment.

Where evidence from spawner-recruit analysis suggests substantial MDN effects on productivity, the development of better forecasting models may be an important first step in adapting improved management practices. Forecasting would provide a conservative approach that allows managers, and stake holders, to evaluate whether those models predict future salmon returns better than current models without instituting disruptive changes to current practices. This approach has been undertaken in Washington state where Pink Salmon escapements are used to predict Coho Salmon smolt production

(Zimmerman 2011), and in Ford Arm Creek (Southeast Alaska) where Pink Salmon escapements are used to predict adult Coho Salmon returns (Shaul et al. 2014). I believe the findings in this dissertation justify the development of such models for the Norton Sound region.

Where improved forecasting and thorough examination of spawner-recruit relationships suggests that the incorporating MDN into management may improve the sustainability and productivity of salmon stocks, it may be necessary to alter harvests and escapement goals. Alaska's salmon fisheries are currently managed for maximum-sustained yield (MSY) and the Alaska Department of Fish and Game sets escapement goals for different species and watersheds to achieve this (Munro and Volk 2015). Escapement goals provide a target number of spawners to achieve on the spawning grounds and harvests may be curtailed by fisheries managers to achieve those goals. Developing spawner-recruit models that incorporate escapements of conspecifics and other species will require identifying new MSYs for those models and subsequently identifying appropriate escapement goals that may differ significantly from those currently established. Where interspecific MDN interactions are considered, this may involve identifying MSY for multiple species using linked models. Changing escapement goals can be contentious if it alters or restricts fishing and will ultimately require cost-benefit analyses to determine if future increases in productivity are worth forgoing present harvests. To get buy-in from stake holders, biologists and managers will need compelling arguments to convince user groups that such changes will benefit them in the long term.

Summary

This dissertation has provided compelling evidence demonstrating interspecific MDN enhancement of salmon productivity and provides a roadmap for further avenues of research including more applied research by management agencies. Long term studies, examinations of juvenile survival and abundance, and retrospective analysis of other salmon species population dynamics should be considered priorities for investigations of MDN's role in salmon productivity. Management agencies may begin exploring modified spawner-recruit models that incorporate MDN relationships between species to determine how

escapement goals would change. Indeed, most salmon fisheries are managed in a single-species framework and MDN based relationships provide an avenue for exploring multispecies management.

Literature Cited

Adkison, M. A. 2010. Models of the effects of marine-derived nutrients on salmon (*Onchorhynchus* spp.) population dynamics. Canadian Journal of Fisheries and Aquatic Science 67: 5-15.

Beamish, R. J., C. Mahnken and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. Transactions of the American Fisheries Science 133: 26-33.

Brakensiak, K. E., and D. G. Hankin. 2007. Estimating overwinter survival of juvenile Coho Salmon in a northern California stream: accounting for effects of passive interated transponder tagging mortality and size-dependent survival. Transactions of the American Fisheries Society 136: 1423-1437.

Brown, R. J., R. J. Henszey, A. von Finster, and J. H. Eiler. 2017. Catalog of Chinook Salmon spawning areas in the Yukon River basin in Canada and the United States. Journal of Fish and Wildlife Management 8: 558-587.

Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Science 68: 232-240.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 47: 2181-2194.

Howard, K., J. M. Murphy, L. Wilson, J. Moss, and E. V. J. Farley. 2016. Assessing size selective mortality of juvenile Yukon River Chinook Salmon using retrospective scale analysis. North Pacific Anadromous Fisheries Commision Bulletin 6.

Menard, J., J. Soong, S. Kent, and A. Brown. 2013. 2012 Annual management report Norton Sound – Port Clarence Area, and Arctic-Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 13-28, Anchorage.

Munro, A. R. 2018. Summary of Pacific salmon escapement goals in Alaska with a review of escapements from 2009 to 2017. Alaska Department of Fish and Game, Fishery Manuscript Series no. 18-04, Anchorage.

Munro, A. R. and E. C. Volk. 2015. Summary of Pacific salmon escapement goals in Alaska with a review of escapements from 2006 to 2014. Alaska Department of Fish and Game, Fishery Manuscript Series No. 15-34, Anchorage.

Nelson, M. C. and J. D. Reynolds. 2014. Time-delayed subsidies: interspecies population effects in salmon. PLoS ONE 9(6): e98951.

Ohlberger, J., S. J. Brenkman, P. Crain, G. R. Pess, J. J. Duda, T. W. Buehrens, T. P. Quinn, and R. Hilborn. 2018. A Bayesian lie-cycle model to estimate escapement at maximum sustained yield in salmon based on limited information. Canadian Journal of Fisheries and Aquatic Science. Published on the web 17 May 2018, https://doi.org/10.1139/cjfas-2017-0382.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson and T. P. Quinn. 2011. The influence of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. Transaction of the American Fisheries Society 140: 883-897.

Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Science 53: 1555-1564.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology, 86 (12), 3225-3231.

Tattam, I. A., J. R. Ruzycki, J. L. McCormick, and R. W. Carmichael. 2015. Length and condition of wild Chinook Salmon smolts influence age at maturity. Transactions of the American Fisheries Society, 144: 1237-1248.

Uchiyama, T., B. P. Finney, and M. D. Adkison. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Onchorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Science 65: 1635-1648.

Walker, B. M., and T. M. Sutton. 2016. Growth-increment formation using otoliths and scales for age-0 Chinook Salmon. North American Journal of Fisheries Management 36: 995-999.

Zabel, R. W. and S. Achord. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. Ecology, 85; 795-806.

Zimmerman, M. 2011. 2011 wild coho forecasts for Puget Sound, Washington Coast, and Lower Columbia. Washington Department of Fish and Wildlife, Olympia, Washington.